# ANALYSIS OF THE FLORA OF MEDITERRANEAN AND SAHARAN AFRICA[1]

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ABSTRACT

After defining the state of knowledge and reviewing national inventories, the author looks at the reasons which led him to study Mediterranean and Saharan Africa and to detail their biogeographical significance.

For Mediterranean and Saharan Africa, the generic and specific richness, the richness of endemics, and the entire biogeographical range are first analyzed at the family level. In the second part, the various biogeographical elements which play a part in the formation of the floras at the generic and specific levels are defined; several examples are provided respectively for the Mesogean (Mediterranean, Saharo-Arabian and Irano-Turanian) and tropical elements. A third part is devoted to endemism: first generic and specific endemism, then the biogeographical significance of the endemic taxa. It appears that the flora of Mediterranean Africa is about three times richer than that of Saharan Africa and that endemism there is two times greater. Whereas the flora of Mediterranean Africa is for the most part made up of Mediterranean taxa, in Saharan Africa there is a nearly equal distribution of Mediterranean, Saharo-Arabian, and tropical elements. These characteristics are related to the hostile ecological conditions which govern the Sahara now, but also reflect the climatic disturbances which took place during the Pleistocene. A special chapter is devoted to a discussion of the historical interpretation of the flora of Mediterranean and Saharan Africa, taking into account the new data provided by paleoclimatology and paleobotany. It is concluded that the Mediterranean flora is relatively old and goes back at least as far as the middle Miocene, whereas the present Saharan flora is a reflection of intense climatic changes which have severely affected this region since the Pliocene. In each of these cases emphasis has been placed on the role elements of African origin played in the development of the present flora.

## I—INTRODUCTION

A little more than the northern quarter of the African continent escapes tropical floristic influences. This rather heterogeneous unit poses many problems of biogeographical and historical interpretation, but is nevertheless rather well known from the point of view of floristic composition.

The territory covered by this study includes the whole of Mediterranean Africa, but also the Sahara down to its southern limits, some close approximations of which will be defined below.

It seemed more meaningful and realistic to abandon the artificial framework of political boundaries for the infinitely more realistic one of biogeographical units.

### I. 1—THE LEVEL OF KNOWLEDGE

In the Maghreb the present state of floristic knowledge of vascular plants, which alone are discussed in this work, can be considered satisfactory such as was stated in the recent symposium of the Centre National de la Recherche Scientifique devoted to the flora of the Mediterranean basin held in Montpellier,

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ANN. MISSOURI BOT. GARD. 65: 479–534. 1978.

0026-6493/78/0479–0534/$05.75/0

1974. Without going into detail, it should be remembered that the state of our knowledge is being published in the *Flore de l'Afrique du Nord* by R. Maire (1952–1976), and that 14 volumes of it have already appeared. Various catalogs and regional floras also reflect floristic knowledge relating to the countries of the Maghreb. For example Jahandiez & Maire (1931–1934), Emberger & Maire (1941), Sauvage & Vindt (1952, 1954) for Morocco, Quézel & Santa (1962–1963) for Algeria, Cuénod (1954) for Tunisia, and Ozenda (1958) for western and central Sahara.

In Libya and in Egypt valuable data are also available (Boulos, 1975) from several publications, in particular for Libya those of Durand & Baratte (1910) and of Pampanini (1931), and for Egypt those of Täckholm (1956, 1974).

On the other hand, for the countries situated further south in the Saharan region, data are much sparser, and one is often obligated to consult partial inventories. The list of these (Quézel, 1965) has not undergone significant modification since Quézel (1965), with the exception of the work by Scholz (1966, 1974) and Scholz & Gabriel (1973).

### I. 2—NATIONAL INVENTORIES

This approach, although not very significant, deserves nevertheless to be considered because it furnishes a preliminary idea of the floristic richness of Northern Africa.

For the countries of the Maghreb, Sauvage (1975) estimates that Morocco has approximately 3,700 species distributed among 920 genera and 124 families. For Algeria and Tunisia (Quézel & Bounaga, 1975), there are about 3,300 species (about 3,100 for Algeria and 2,100 for Tunisia, Le Houérou, 1975) 980 genera and 130 families. As for Libya (Boulos, 1975), it has approximately 1,600 species and Egypt somewhat more than 2,000 (including Sinai).[2]

In contrast, it is difficult to state exactly the floristic richness of the countries of the Sahel, a part of which territory is to be considered here. Saharan Mauritania and the former Spanish Sahara have a flora which can reasonably be estimated (Guinea, 1949; Monod, 1938, 1939, 1952; Murat, 1944; Sauvage, 1946, 1949; Naegele, 1958) at about 600 species. The figures are even smaller for Saharan Mali and Niger (probably less than 250 species). Northern Chad, however, due to the relative richness of Tibesti (Maire & Monod, 1950; Quézel, 1958) has at least 550 species. Saharan Sudan was not included in this work, but besides the mountains adjacent to the Red Sea, which represent a very special case, the real Saharan zone of this country probably has no more than 200 species.

### I. 3—THE LIMITS OF THE ZONE STUDIED

Even though nearly all biogeographers who have worked in northern Africa agree on a general interpretation of the major limits (Monod, 1957; Quézel, 1965; Barry et al., 1976), a certain number of problems deserve, nevertheless, to be stated and discussed. One point that is particularly important is to trace

[2] The Sinai Peninsula, being situated geographically in Asia, will not be considered here.

the limits between the Holarctic Floristic Kingdom and the Paleotropical Floristic Kingdom.

It should be remembered that the Holarctic Kingdom in northern Africa is represented by two floristic regions: the Mediterranean Region and the Saharo-Sindian, or better, Saharo-Arabian (sensu Zohary, 1973) Region. The existence of vestiges or Irano-Turanian relicts, discussed especially by Zohary (1962), seems difficult to accept for bioclimatic, floristic, or dynamic reasons. Actually, these regions have numerous common characteristics, and biogeographers are more and more tempted to put them under one subkingdom which may most appropriately be called the "Mesogean." This viewpoint, already suggested by Gaussen (1954) and accepted from the standpoint of bioclimates by Emberger (1945), Daget (1977), and Nahal (in particular 1976), underlies the narrow genetic and historical affinities that exist in the entire domain of the old Tertiary Mesogean (Tethys).

Be that as it may, and without going into discussions which go well beyond the limits of this study, and without establishing limits too strictly, it is possible and practical to accept the isohyet of 100 mm (Capot-Rey, 1953; Quézel, 1965) to limit the southern extension of the Mediterranean Region.

It is evident that this arbitrary boundary corresponds well to ecological and biogeographical realities, in spite of many exceptions, and also in spite of the opinion of Emberger (1945) and, more recently, Barry et al. (1976) who tend to move the boundary of the Mediterranean Region to the south, essentially for bioclimatic reasons for the first author (annual rainfall pattern still of a Mediterranean type) or genetic reasons for the second authors (flora still rich in Mediterranean elements). I would prefer to call it "Mesogean."

One must recognize, however, that the problem of the boundaries between the Saharo-Arabian Region and the Sudano-Angolan Region, and in fact between the Holarctic and Paleotropical Kingdoms (Monod, 1957) is much more difficult to resolve. Indeed, as I have shown (Quézel, 1965), whereas a large portion of the Sahara belongs, for the most part, to the Saharo-Arabian Region, toward the south the question becomes complicated by the extension, or even predominance, of the elements of tropical origin (without forgetting residual Mediterranean taxa, particularly on high Saharan mountains). These characteristics are basically connected to the large climatic fluctuations that took place in the Sahara during the entire Quaternary, and of which the latest changes are quite close to us, probably less than 5,000 years (Pons & Quézel, 1956, 1957; Quézel & Martinez, 1961), and brought with them vast floristic mixing. The effects of these changes are still being felt. Its interpretation could scarcely be established at anything other than the level of a precise analysis of present ecological factors. These difficulties led us to define as "regional complexes"[3] areas where Saharan, tropical, or even Mediterranean floristic elements coexist in more or less equal numbers.

It is certainly appropriate to keep the flora of the zonal complexes, "Mediter-

[3] One hears today the term "zonal complexes," a term whose biogeographical value is less precise.

TABLE 1. Phytogeographical subdivisions of the flora of North Africa.

| | HOLARCTIC KINGDOM | | | | | PALEOTROPICAL KINGDOM | |
|---|---|---|---|---|---|---|---|
| | Mesogean Subkingdom | | | | | African Subkingdom | |
| | Mediterranean Region | | Saharo-Arabian Region | Complex Zones | | Soudano-Angolan Region | |
| | West-Mediterranean Subregion | East-Mediterranean Subregion | Saharan Subregion | Mediterranean-Saharo-Sudanian Complex Zone | Saharo-Sudanian Complex Zone | Saharo-African Subregion | Sahelian Subregion |
| DOMAINS | Mediterranean North-African (1)<br>Steppic North-African (2) | Cyrenian North-African (3)<br>Steppic Eastern-African (4) | N.W. Saharan (5)<br>N. Saharan (6)<br>Oceanic Saharan (7)<br>N.E. Saharan (8) | Saharan High Mountains (9) | Central Saharan (10)<br>Eastern Saharan (11)<br>Western Saharan (12) | Southern Saharan (13) | Northern Sahelian (14) |

ranean-Saharo-Arabian-Sudano-Angolan" (high Saharan mountains) and Saharo-Arabian-Sudano-Angolan (western, central and eastern Sahara) in the framework of this study. However, the case of the southern Saharan fringe (southern Sahara) can be disputed. That zone is characterized by a very poor flora, it is true, but one of essentially African origin which permits its integration into a particular subregion (Saharo-African Subregion). This subregion is included in our study since in physiognomy it much resembles a Saharan country, because its exact boundaries to the north are extremely difficult to state exactly, and because on the floristic level, it actually only has a very small number of species, probably less than 50.

The southern boundary established in this study (with the exceptions noted above) is therefore the physiognomically southern boundary of the Sahara, a boundary which is made real by the appearance of an ephemeral, but nearly continuous plant cover which corresponds noticeably to the 150 mm isohyet (Capot-Rey, 1953; Quézel, 1965).

These biogeographic interpretations have been schematically indicated in Table 1 and Fig. 1.

### I. 4—SOME PROBLEMS RELATING TO FLORISTIC ANALYSIS

If the floristic inventory of northern Africa can be considered, as we have seen, practically completed, certain problems, nevertheless deserve attention.

Indeed, at the outset, from the point of view of nomenclature the study of the flora of North Africa or of the Sahara has not followed that of the European flora, for example, and one has generally stayed with Maire's concepts which, in many cases, are in need of revision. Since this work is currently in progress, it has been difficult to consider it here, except in some classical cases. Nor is that our purpose here.

As in all attempts at synthesis, the results obtained can vary with different conditions, especially according to the species concept. Our point of view is perhaps too narrow, but we have hesitated to accept a certain number of still debatable positions concerning certain critical genera. The case of the genus *Rupicapnos* is probably the most obvious. Pugsley (1917) recognized some 30 species of it in North Africa, nearly one per locality. The arguments and the criticisms of this author remain debatable, in particular if one studies the question at the population level and not by herbarium specimens, and following Maire (1952–1976) only three species are kept in this genus.

Certain critical genera are also very poorly known, in particular in the Maghreb. For example, it is evident that the 10 species kept in the genus *Rubus*, the 12 in *Rosa*, or the dozen in *Hieracium* or *Crepis* are, from all evidence, very much below what is actually there.

Likewise, a precise taxonomic analysis will certainly lead to a revision of our position on the value of a certain number of genera and species, whether they might be synonymized specifically with certain taxa of the Near East, or whether entities currently considered homogeneous might be separated.

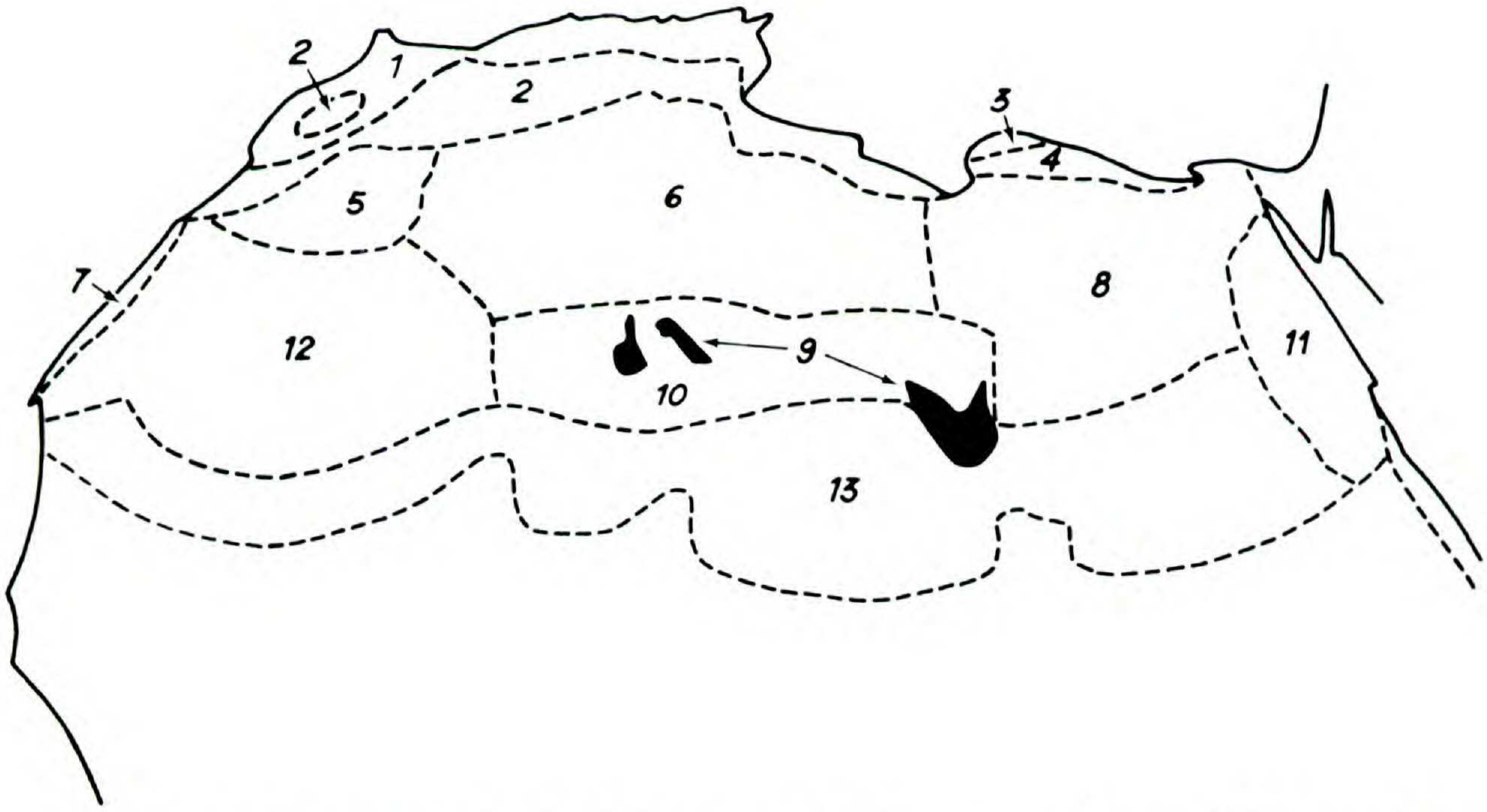


FIGURE 1. Phytogeographical subdivisions of Mediterranean Africa and Saharan Africa. —1. Mediterranean-Northern African Domain.—2. Steppic-Northern African Domain.—3. Cyrenian-Mediterranean Domain.—4. Steppic-Eastern African Domain.—5. Northwestern-Saharan Domain.—6. Northern Saharan Domain.—7. Oceanic Saharan Domain.—8. Northeastern Saharan Domain.—9. Saharan-High Mountain Domain.—10. Central Saharan Domain. —11. Eastern Saharan Domain.—12. Western Saharan Domain.—13. Southern Saharan Domain.—14. Northern Sahelian Domain.

In view of this, the figures provided below can only be considered to be estimates. They are, however, significant because, despite these reservations, the fact remains that the Mediterranean African and Saharan floras are the best known and most studied on the African continent.

Therefore we shall study below and successively the floras of Mediterranean and Saharan Africa. This plan will obviously lead to the appearance of a certain number of species in the two chapters; in fact, this number is not very high and does not exceed 200. Likewise, some tropical species present in the southern Sahara especially will reappear in the statistics for tropical Africa. Here again the number of these species is not very large and probably even less than the number referred to above.

Finally let us note that a certain number of difficulties appeared during the establishment of the biogeographical spectrum. It is basically the problem presented by "connecting" (Eig, 1931) species of two or more regions. Without extending their interpretation too far, they have generally been partially counted at the level of biogeographical groups (0.5 and 0.5, for example, for a connecting Saharan-tropical species). We have, however, avoided showing decimals in the summary tables, decimals which would have given an unwarranted impression of precision. Also we have not taken into account the species obviously adventive or introduced by man, and whose naturalization cannot be established.

## II.—MEDITERRANEAN AFRICA

Mediterranean Africa includes mainly the three countries of the Maghreb to the north of the southern edge of the Bani and the Saharan Atlas, as well as the Libyan coastline (including the Djebel Nefoussa in Tripolitaine and Akhbar in Cyrenaïque), and the Egyptian coastline, covering an area on the order of 900,000 km$^2$.

The countries of the Maghreb, which represent about 800,000 km$^2$ of the total, constitute far and away the most remarkable unit, the richest from the floristic point of view, and one in which historical and geomorphological factors have allowed the development of the greatest number of endemics. The eastern unit (Libya and Egypt) is infinitely poorer and less diversified, but still presents several problems which will be examined later on.

## II. 1—THE FAMILIES

### II.1.1—*Generic and Specific Richness* (Table 3)

In Mediterranean Africa, 130 families of phanerogams and 18 families of vascular cryptogams are represented.

Their generic representation is quite variable, and only 2 families have more than 100 genera (Gramineae 114, Compositae 106), 2 have more than 50 (Cruciferae 84, Umbelliferae 61), 5 more than 20 (Leguminosae 49, Labiatae 34, Caryophyllaceae 32, Boraginaceae 26, Liliaceae 24), and 6 more than 10 (Chenopodiaceae 19, Rosaceae 19, Scrophulariaceae 18, Orchidaceae 13, Ranunculaceae 13, Papaveraceae 11); the Filicales contain 15 genera. Fourteen families have from 6 to 10 genera, 52 have 2 to 5, and 55 have only one.

From the standpoint of richness of species only 8 families exceed 100 species: Compositae 563, Leguminosae 432, Gramineae 338, Caryophyllaceae 227, Labiatae 222, Cruciferae 215, Scrophulariaceae 145, and Liliaceae 113. Ten families have between 99 and 50 species: Boraginaceae 86, Cyperaceae 80, Ranunculaceae 64, Euphorbiaceae 62, Cistaceae and Rosaceae 60, Chenopodiaceae 58, Orchidaceae 54, Papaveraceae 52, and Rubiaceae 50. Fifteen families have 49 to 20 species: Geraniaceae 47, Plumbaginaceae 46, Crassulaceae 43, Orobanchaceae 40, Campanulaceae 37, Polygonaceae 36, Iridaceae and Malvaceae 32, Convolvulaceae 31, Juncaceae 29, Valerianaceae 26, Resedaceae 25, Dipsacaceae 24, Plantaginaceae 23, and Amaryllidaceae 20. Altogether the Filicales contain 37 species. Fifteen families possess 19 to 10 species: Linaceae, Saxifragaceae and Solanaceae 18, Thymelaeaceae 17, Gentianaceae and Primulaceae 16, Onagraceae 14, Potamogetonaceae 12, Aizoaceae, Amaranthaceae, Asclepiadaceae and Caprifoliaceae 11, Salicaceae, Violaceae and Zygophyllaceae 10.

Without carrying this analysis further, it is appropriate to point out that 10 families are represented by 4 species, 11 by 3, 18 by 2 and 28 are monospecific in Mediterranean Africa.

### II.1.2—*Biogeographical Significance at the Family Level*

Without entering further into an exact analysis, and without considering the biogeographical value of the endemics, it is nevertheless worthwhile to point out that in Mediterranean Africa, the great majority of families is essentially made up of species linked to the Mediterranean element. However, several exceptions should be noted.

Thus the major element is no longer Mediterranean but "northern" in the following families of several species: Aceraceae, Alismataceae, Betulaceae, Callitrichaceae, Ceratophyllaceae, Cyperaceae, Elatinaceae, Grossulariaceae, Haloragidaceae, Hydrocharitaceae, Juncaceae, Juncaginaceae, Lemnaceae, Lentibulariaceae, Loranthaceae, Nymphaeaceae, Onagraceae, Orchidaceae, Primulaceae, Ranunculaceae, Rosaceae, Salicaceae, and Sambucaceae. The same is true for the following monospecific families: Adoxaceae, Aquifoliaceae, Araliaceae, Butomaceae, Dioscoreaceae, Illecebraceae, Juglandaceae, Menyanthaceae, Monotropaceae, Najadaceae, Parnassiaceae, Sparganiaceae, and Taxaceae. The majority of these families is essentially composed of aquatic or largely hygrophilous taxa which escape climatic influences, or have only a small number of species, which creates a deceptive statistical interpretation. The Rosaceae, Ranunculaceae, Orchidaceae, and Primulaceae deserve mention; these relatively important families are in fact the only families in Mediterranean Africa that have a predominance of elements of northern stock.

Also mentioned should be families in which the majority of the species are related to cosmopolitan or more or less ubiquitous lines: Aizoaceae, Amaranthaceae, Hydrocharitaceae (already cited above), Najadaceae, Nyctaginaceae, Onagraceae, Oxalidaceae, Polygonaceae, Portulacaceae, Potamogetonaceae, Typhaceae, Trappaceae, Verbenaceae, and Zosteraceae. Here again mainly aquatic or even clearly anthropophilous (?) families predominate; the Aizoaceae and the Nyctaginaceae have, however, tropical affinities.

### II.1.3—*Endemic Richness at the Family Level*

Endemic richness is quite variable. If limited to a strict inventory, the figures are the following: more than 100 endemic species: Compositae 231, Leguminosae 105; more than 50 endemic species: Labiatae 99, Caryophyllaceae 75, Cruciferae 72, Umbelliferae 53, Scrophulariaceae 50; more than 20: Gramineae 42, Liliaceae 25, Boraginaceae 23; more than 10: Geraniaceae and Plumbaginaceae 17, Campanulaceae 16, Crassulaceae and Euphorbiaceae 13, Cistaceae, Papaveraceae and Resedaceae 11, Ranunculaceae 10; more than 5: Iridaceae and Orobanchaceae 9, Chenopodiaceae, Convolvulaceae and Rubiaceae 8, Dipsacaceae, Linaceae and Saxifragaceae 7, Malvaceae and Rosaceae 6, Orchidaceae and Polygonaceae 5; with 4 endemic species: Amaryllidaceae, Plantaginaceae, Thymelaeaceae, Valerianaceae and Violaceae; with 3 endemic species: Gentianaceae, Onagraceae, Polygalaceae, and Zygophyllaceae; with 2 endemic species: Aizoaceae, Asclepiadaceae, Hypericaceae, Primulaceae, Santalaceae, and Selaginaceae. Finally the following families are represented by only one endemic species: Anacardiaceae, Araceae, Berberidaceae, Capparaceae, Caprifoliaceae, Commelinaceae, Fagaceae, Frankeniaceae, Juncaceae, Najadaceae, Pinaceae, Rutaceae, Sapotaceae, and Solanaceae.

Sixty-nine families have no endemic species in Mediterranean Africa. Among

TABLE 2. Distribution of the total number of species in Mediterranean Africa into its biogeographical subdivisions.

| Subdivision | Number | Percentage (%) |
|---|---|---|
| Total genera | 916 | |
| Total species | 4034 | |
| Endemics | 1038 | 25.7 |
| North African | 78 | 1.9 |
| Ibero-Mauritanian | 408 | 10.1 |
| Macaronesian | 27 | 0.5 |
| Western Mediterranean | 321 | 7.9 |
| Eastern Mediterranean | 160 | 3.9 |
| Mediterranean | 873 | 21.6 |
| Irano-Turanian | 33 | 0.8 |
| Saharo-Sindian | 122 | 3.0 |
| Atlantic | 63 | 1.5 |
| European and Eurasian | 528 | 13.1 |
| Paleotemperate | 73 | 1.8 |
| Circumboreal | 40 | 0.9 |
| Tropical | 56 | 1.3 |
| Cosmopolitan or other distribution | 214 | 5.3 |

these, only 5 are represented by more than 10 species. They are the following: Cyperaceae 80, Potamogetonaceae 12, Amaranthaceae 11, and Salicaceae and Tamaricaceae 10.

### II.1.4—*The Global Biogeographical Spectrum*

For the entire flora of Mediterranean Africa, maintaining the accepted biogeographical subdivisions, the percentages are given in Table 2.

## II.2—THE PRINCIPAL BIOGEOGRAPHICAL ELEMENTS

We shall look at them successively, ending with a study of the endemics.

### II.2.1—*Mediterranean Taxa*

II.2.1.1—*Ibero-Mauritanian Taxa.*—Ibero-Mauritanian taxa represent about 10% of the Mediterranean African flora, and naturally are found principally in the Maghreb. Regrouped under this heading are the following (Quézel, 1957) elements: Ibero-Mauritanian, in the strict sense, Betico-Atlas and Pyrenees-Atlas. Differentiation of these three groups is not always easy, but schematically they certainly correspond to different groups.

The Ibero-Mauritanian group is present in more than half of the families; however, it plays a particularly important role in the following families, where it represents percentages greater than 10:[4] Liliaceae: *Braxireon**; Amaryllidaceae: *Leucojum*, *Lapiedra**, *Narcissus*; Boraginaceae: *Echium*; Campanulaceae: *Campanula*, *Jasione*; Caryophyllaceae: *Arenaria*, *Minuartia*, *Silene*; Cistaceae: *Cistus*, *Helianthemum*, *Halimium*; Compositae: *Senecio*, *Centaurea*, *Andryala*, *Carduus*,

[4] The Ibero-Mauritanian genera are followed by an asterisk.

*Prolongoa**, *Otospermum**, *Daveaua**, *Glossopappus**; Crassulaceae: *Sedum*; Cruciferae: *Diplotaxis*, *Alyssum*, *Matthiola*; Ericaceae; Euphorbiaceae: *Euphorbia*; Gramineae; Iridaceae: *Iris*, *Romulea*, Labiatae: *Teucrium*, *Thymus*; Leguminosae: *Retama*, *Stauracanthus*, *Erinacea**, *Ulex*, *Cytisus*, *Genista*, *Ononis*, *Anthyllis*; Malvaceae; Orobanchaceae; Plumbaginaceae; Rosaceae; Rubiaceae; Saxifragaceae; Solanaceae: *Triguera**; Saxifragaceae; Scrophulariaceae: *Linaria*, *Odontites*; Thymelaeaceae; Umbelliferae: *Eryngium*, *Ammiopsis**, *Brachyapium*, *Bupleurum*; Valerianaceae; Papaveraceae: *Sarcocapnos**, *Rupicapnos**, *Platycapnos*, *Ceratocapnos*.

Here are some particularly significant examples at the species level:

Betico-Rifaines species: *Abies pinsapo*, *Drosophyllum lusitanicum*, *Eryngium glaciale*.

Betico-Atlas species: *Anthyllis warnieri*, *Arenaria pungens*, *Andryala aghardii*, *Sedum melanantherum*, *Pseudocytisus integrifolius*, *Poterium ancistroides*.

Pyrenees-Atlas species: *Potentilla alchimilloides*, *Matthiola perennis*, *Valeriana globulariaefolia*, *Saxifraga longifolia*, *Lonicera pyrenaica*.

II.2.1.2—*Macaronesian Taxa*.—In Mediterranean Africa, Macaronesian taxa are mainly found on the Atlantic coast of Morocco, especially in the Sous valley. They represent (without counting the endemics of Macaronesian stock) less than 30 species. Especially important are the following: *Davallia canariensis*, *Asparagus pastorianus*, *Traganum moquini*, *Chenolea tomentosa*, *Euphorbia balsamifera*, *E. obtusifolia*, *Helianthemum canariense*, *Polycarpaea nivaea*, *Drusa oppositifolia*, *Astydamia latifolia*, *Zygophyllum fontanesii*, *Hypericum coadunatum*, *Rhus albida*, *Lithospermum microspermum*, *Carraluma buchardii*, *Phagnalon calycinum*, *Asteriscus odorus*, *Andryala canariensis*, and *Sonchus pinnatifidus*.

II.2.1.3—*Western Mediterranean Taxa*.—Slightly less numerous than the Ibero-Mauritanian (321), the Western Mediterranean taxa still represent approximately 8% of the entire flora. Actually, also included here are a certain number of Centro-Mediterranean or even Tyrrhenian elements, which are not very abundant and from which it is appropriate to cite in particular: *Silene sedoides*, *Rosa serafini*, *Vicia barbazitae*, *Sideritis romana*, *Stachys marrubiifolia*, and also the genus *Tetragonolobus*.

The Western Mediterranean taxa are especially frequent in the following families: Boraginaceae 6, Caryophyllaceae 20, Cistaceae 11, Compositae 52, Cruciferae 12, Euphorbiaceae 9, Gramineae 21, Labiatae 19, Leguminosae 43, Liliaceae 15, Scrophulariaceae 11, and Umbelliferae 12.

Among the genera especially representative of this biogeographical subdivision are: *Chamaerops*, *Ampelodesmos*, *Avellinia*, *Wangenheimia*, *Aphyllanthes*, *Ionopsidium*, *Succowia*, *Solenanthus*.

II.2.1.4—*Northern Mediterranean Orophilous Taxa*.—Some species, in general largely present on the mountains of the northern Mediterranean slope from which they spread northward, strangely appear in North Africa only on numidic mountains. Such is the case for *Juniperus sabina*, *Alopecurus gerardii*, *Anthyllis montana*, *Scabiosa crenata*, *Daphne oleoides*, *Sedum majellense*, *Saponaria depressa*, *Euphorbia luteola*, *Campanula trichocalycina*, *Robertia taraxacioides*. Their placement is probably more recent than that of the oro-endemics of the Atlas, and their migration by the Sicilian-Tunisian bridge in the Pleistocene is likely.

II.2.1.5—*Eastern Mediterranean Taxa.*—Eastern Mediterranean taxa include 160 species representing about 4% of the flora. Of course the eastern Mediterranean element is especially prominent in Libya and in Egypt where it is represented by such genera as *Sarcopoterium* and *Thymbra*, but especially by annual species belonging to the genera *Silene*, *Erysimum*, *Trifolium*, *Trigonella*, and *Verbascum*.

II.2.1.6—*Circum-Mediterranean Taxa.*—Circum-Mediterranean taxa represent the largest group (after the endemics) with 873 species and nearly 22% of the entire flora. It is unnecessary to dwell on this group, which correlates almost exactly with the entire flora from the point of view of family and generic representation.

However, a group of species should be pointed out which is included here, but which in fact show an element of the Mesogean type. Their distribution area stretches from the Atlantic to the western Himalaya. Among these species, most belong to orophilous lines. Their distribution resembles that of the genus *Cedrus* (Fig. 2). In particular may be noted: *Fraxinus xanthoxyloides*, *Prunus prostrata*, *Cotoneaster nummularia*, and *Scutellaria orientalis* (Quézel, 1957; Meusel, 1971).

Because of the age of their disjunction, these species are polymorphic. Indeed, this type of distribution is found especially in the endemo-vicariants series (cf. below).

### II.2.2—*The Irano-Turanian Taxa*

There are hardly more than 30 Irano-Turanian taxa (without counting the endemics which belong to this biogeographical subdivision). This weak representation certainly confirms the absence of this region in North Africa and especially on the high plateaus of the Maghreb. It is nevertheless interesting to note that it is the Chenopodiaceae which have the greatest number of species belonging to this element. In particular may be noted: *Kochia prostrata*, *Anabasis aphylla*, *Noaea mucronata*, *Salsola paletzkiana*.

### II.2.3—*Saharo-Arabian Taxa*

A little more than 120 species (3%) of the flora represent the Saharo-Arabian element in Mediterranean Africa. These species are not particularly interesting biogeographically. They nearly always represent southern infiltrations into the most arid part of the Mediterranean region of Hodna in Algeria and into the middle valley of the Moulouya in Morocco.

### II.2.4—*Taxa of Northern Origin*

Among the Northern taxa are included the Atlantic (63, 1.5%), European and Eurasian (528, 13.1%), Paleotemperate (74, 1.8%), and Circumboreal (40, 1%) taxa. Without going into detail, the predominance of European and Eurasian taxa may be noted. These make up a large contingent which is commonly

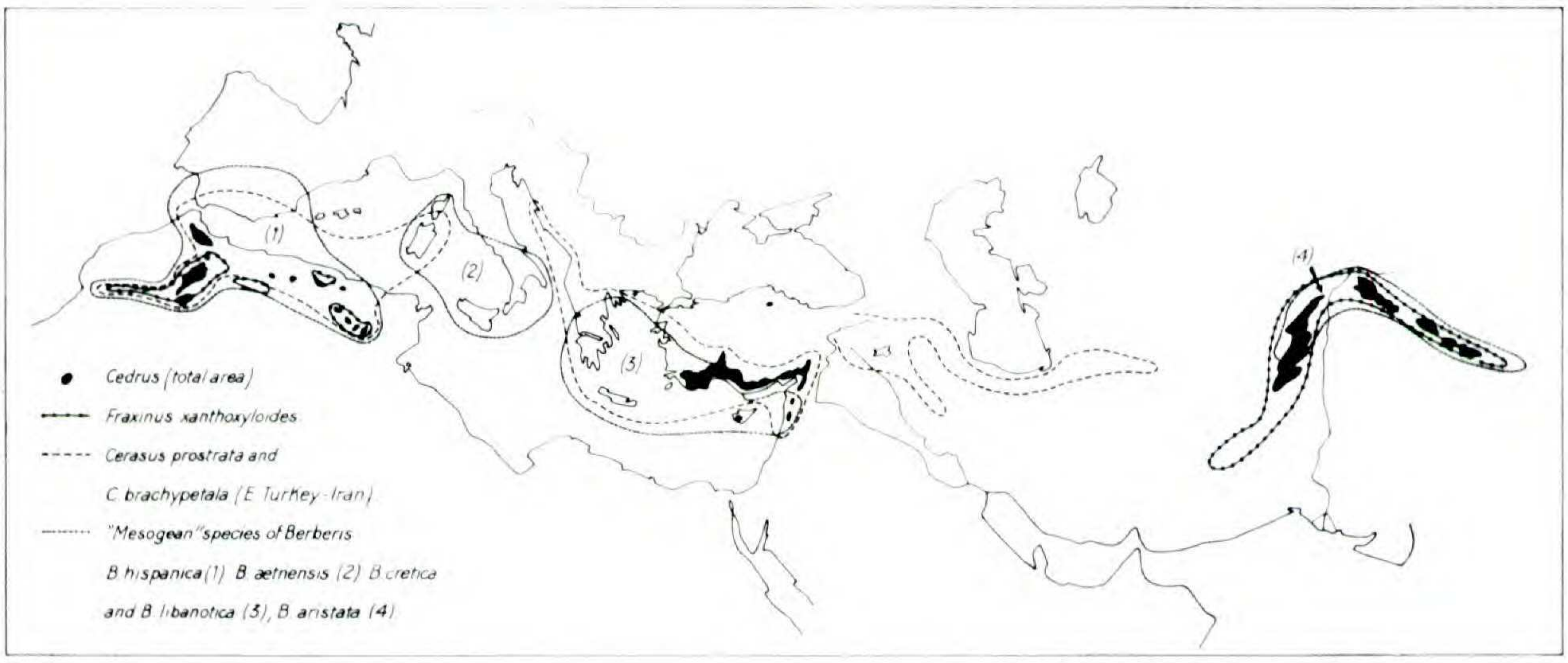


FIGURE 2. Distribution of circum-Mediterranean taxa.

found in the wettest zones of the North African tells, particularly at the edge of water and in forest associations. Among the most noteworthy genera are: *Cyperus*, *Scirpus*, *Juncus*, *Salix*, *Ranunculus*, *Papaver*, *Fumaria*, *Sedum*, *Potentilla*, *Geranium*, *Acer*, *Anthriscus*, *Oenanthe*, *Caucalis*, and *Veronica*.

A certain number of orophilic species also belong to this group; the most representative are (without counting the phenomenon of microendemism): *Calamagrostis argentea*, *Agrostis alpina*, *Avena montana*, *Blysmus compressus*, *Aquilegia vulgaris*, *Aconitum lycoctonum*, *Draba tomentosa*, *Rhamnus pumilla*, *Meum athamanticum*, *Androsace villosa*, *Gentiana verna*, *Euphrasia minima*, *Galium pumilum*, and *Asperula odorata*.

The circumboreal element, although weakly present, also appears mostly on high mountains, the Atlas in particular, and, by its presence, poses interesting historical problems. As I have shown (Quézel, 1957), this element generally represents the vestiges of a flora which came into North Africa at the glacial periods and which arrived almost exclusively by way of the Iberian Peninsula, perhaps bird dispersal playing a small role. Among the most noteworthy representatives are: *Botrychium lunaria*, *Dryopteris lonchitis*, *Nardus stricta*, *Polygonum bistorta*, *Carex capillaris*, *Luzula spicata*, *Luzula multiflora*, *Cerastium cerastioides*, *Sagina saginoides*, *Viola palustris*, *Gentiana tenella*, and *Parnassia palustris*.

The Atlantic element is especially well represented in Morocco, but it is also found along the Algero-Tunisian coast. Among the most notable types are the genera: *Chaeturus*, *Airopsis*, *Antinoria*, *Periballia*, *Gratiola*, *Illecebrum*, and *Quercus pyrenaica*.

### II.2.5—*Taxa of Tropical Origin*

It is appropriate to expand somewhat on the tropical taxa, particularly within the framework of a total floristic and biogeographical interpretation of the African continent.

According to the figures, they represent a small group in Mediterranean

Africa (excluding the Nile Delta) with about 55 species and 1.3% of the flora. Without considering here the problem of Mediterranean endemics of tropical origin, a study of Table 3 shows immediately that two families alone contain more than half of these species: the Gramineae (24) and the Cyperaceae (8). In fact, an even higher number could be envisaged if one takes into account many of them which are connecting (?) Sudano-Angolan-Mediterranean species.

Among the latter, many correspond to hygrophytes, or even hydrophytes, whose presence in Mediterranean Africa can be linked to transport by migratory birds (at least for some of them). There are in particular, and mainly for the marshes of the Moroccan or Calle coast, several representatives of the genera *Cyperus* (*C. michelianus*, *C. polystachyos*, *C. corymbosus*), *Fimbristylis* (*F. squarrosa*, *F. dichotoma*), as well as *Rhynchospora alba*, *Fuirena pubescens*, *Polygonum senegalense*, *Typha elephantina*, *Oldenlandia capensis*, *Laurenbergia tetrandra*, *Glinus lotoides*, and *Alternanthera sessilis*.

Numerous annuals linked to cultivation and without great biogeographical interest can also be noted here; they belong principally to the genera: *Sorghum*, *Digitaria*, *Brachiaria*, *Paspalum*, *Paspalidium*, *Echinochloa*, *Panicum*, *Eragrostis*, *Dactyloctenium*, and *Achyranthes aspera*.

Indeed, the most remarkable group is made up of species generally present both in the tropical dry zone and in the Mediterranean region where they are often abundant. They pose an interesting biogeographical problem. The Gramineae and, in particular the Andropogoneae, play a major role here. Most of these probably arrived in the Mediterranean region during the Quaternary pluvial periods. Their path of migration followed the mountain chains adjacent to the Red Sea, but also the high Saharan mountains, and even the Atlantic coast. Among the most noteworthy are (cf. Fig. 3): *Chrysopogon aucheri*, *Andropogon distachyus*, *Hyparrhenia hirta*, *Heteropogon contortus*, *Themeda triandra*, *Tricholaena teneriffae*, *Cenchrus ciliaris*, *Pennisetum setaceum*, *Enneapogon scaber*, *Oropetium africanum* (Gillet & Quézel, 1959), *Dichanthium annulatum*, as well as on the Moroccan coast, *Enteropogon rupestris*.

## II.3—ENDEMISM IN MEDITERRANEAN AFRICA

Successively we shall look at generic and specific endemism and then try to define the biogeographical significance of endemism in the flora of Mediterranean Africa.

### II.3.1—*Generic Endemism*

In spite of several taxonomic uncertainties, it is clear that generic endemism is relatively important in Mediterranean Africa, and especially in the Maghreb. In fact 38 genera can be put into this category, although some, which are present in the Mediterranean region, are more widely represented in the Saharan region, and will be studied later on. These are principally the genera *Oudneya*, *Eremophyton*, *Perralderia*, *Rhanterium*, *Warionia*, and *Tourneuxia*.

Among the remaining 32 genera: 12 belong to the Cruciferae: *Trachystoma*,

TABLE 3. The principal biogeographical elements of the families of Mediterranean Africa. Heading abbreviations are as follows: Gen. = Genera, Sp. = Species, End. = Endemics, N.A. = North African, I.-M. = Ibero Mauritanian, Mac. = Macaronesian, W.-Med. = Western Mediterranean, E.-Med. = Eastern Mediterranean, Med. = Mediterranean, I.-T. = Irano-Turanian, S.-S. = Saharo-Sindian, Atl. = Atlantic, E.&E. = European & Eurasian, Pt. = Paleotemperate, Cb. = Circumboreal, Trop. = Tropical, Oth. = Other.

| Family | Gen. | Sp. | End. | N.A. | I.-M. | Mac. | W.-Med. | E.-Med. | Med. | I.-T. | S.-S. | Atl. | E.&E. | Pt. | Cb. | Trop. | Oth. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Acanthaceae | 1 | 2 | . | . | . | . | . | 1 | 1 | . | . | . | . | . | . | . | . |
| Aceraceae | 1 | 4 | . | . | . | . | . | . | 1 | . | . | . | 3 | . | . | . | . |
| Adoxaceae | 1 | 1 | . | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . |
| Aizoaceae | 6 | 11 | 2 | . | . | . | . | 1 | 1 | . | . | . | . | 4 | . | . | 3 |
| Alismataceae | 3 | 4 | . | . | . | . | 1 | . | . | . | . | 2 | . | . | . | . | 1 |
| Amaranthaceae | 4 | 11 | . | . | . | . | . | . | . | 1 | 1 | . | . | 2 | . | . | 7 |
| Amaryllidaceae | 8 | 20 | 4 | 1 | 4 | . | 3 | . | 5 | . | . | 1 | . | . | . | 1 | 1 |
| Anacardiaceae | 2 | 7 | 1 | . | . | 1 | . | . | 4 | 1 | . | . | . | . | . | . | . |
| Apocynaceae | 2 | 4 | . | . | . | . | 1 | . | 3 | . | . | . | . | . | . | . | . |
| Aquifoliaceae | 1 | 1 | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . |
| Araceae | 6 | 8 | 1 | . | . | . | 1 | . | 6 | . | . | . | . | . | . | . | . |
| Araliaceae | 1 | 1 | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . |
| Aristolochiaceae | 1 | 4 | . | . | 1 | . | 1 | . | 2 | . | . | . | . | . | . | . | . |
| Asclepiadaceae | 6 | 11 | 2 | . | 1 | 1 | . | 1 | 4 | . | 1 | . | 1 | . | . | . | . |
| Balanophoraceae | 1 | 1 | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . |
| Berberidaceae | 3 | 4 | 1 | . | 1 | . | . | 2 | . | . | . | . | . | . | . | . | . |
| Betulaceae | 2 | 2 | . | . | . | . | . | . | . | . | . | . | 2 | . | . | . | . |
| Boraginaceae | 26 | 86 | 23 | . | 1 | 1 | 6 | 8 | 26 | . | 7 | . | 4 | 1 | 2 | 1 | . |
| Butomaceae | 1 | 1 | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . |
| Buxaceae | 1 | 2 | . | . | 1 | . | . | . | 1 | . | . | . | . | . | . | . | . |
| Callitrichaceae | 1 | 3 | . | . | . | . | . | . | . | . | . | . | 2 | . | . | . | 1 |
| Campanulaceae | 9 | 37 | 16 | . | 6 | . | 3 | 2 | 3 | . | . | . | 6 | . | . | . | 1 |
| Capparaceae | 2 | 5 | 1 | . | 1 | . | . | . | 1 | . | 1 | . | . | . | . | 1 | . |
| Caprifoliaceae | 3 | 11 | 1 | . | 1 | . | 2 | . | 8 | . | . | . | 3 | . | . | . | . |
| Caryophyllaceae | 32 | 227 | 75 | . | 28 | 1 | 20 | 9 | 38 | 1 | 11 | 2 | 25 | 2 | 3 | . | 12 |
| Celastraceae | 2 | 2 | . | . | . | . | . | . | 1 | . | . | . | . | . | . | 1 | . |
| Ceratophyllaceae | 1 | 2 | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | 1 |
| Chenopodiaceae | 19 | 28 | 8 | 1 | 3 | 2 | 2 | 1 | 11 | 5 | 7 | . | 5 | . | . | . | 13 |
| Cistaceae | 5 | 60 | 11 | 2 | 13 | 2 | 11 | 2 | 16 | . | 3 | . | . | . | . | . | . |

TABLE 3. *Continued.*

| Family | Gen. | Sp. | End. | N.A. | I.-M. | Mac. | W.-Med. | E.-Med. | Med. | I.-T. | S.-S. | Atl. | E.&E. | Pt. | Cb. | Trop. | Oth. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cneoraceae | 1 | 1 | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . |
| Commelinaceae | 1 | 1 | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Compositae | 106 | 563 | 231 | 5 | 63 | 5 | 52 | 6 | 96 | 2 | 22 | 3 | 45 | 1 | 4 | 2 | 27 |
| Convolvulaceae | 5 | 31 | 8 | . | 1 | . | 4 | 2 | 6 | . | . | . | 2 | 1 | . | . | 7 |
| Coriariaceae | 1 | 1 | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . |
| Cornaceae | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Crassulaceae | 5 | 43 | 13 | . | 6 | . | 1 | 3 | 9 | . | . | 1 | 9 | . | . | 1 | . |
| Cruciferae | 84 | 215 | 72 | 2 | 21 | 2 | 12 | 10 | 40 | 4 | 7 | 2 | 32 | 1 | 1 | . | 9 |
| Cucurbitaceae | 3 | 3 | . | . | . | . | . | . | 1 | 1 | . | . | 1 | . | . | . | . |
| Cupressaceae | 3 | 7 | . | . | . | . | 2 | . | 3 | . | . | . | . | 2 | . | . | . |
| Cyperaceae | 9 | 80 | . | . | 1 | . | 1 | 1 | 5 | . | . | 2 | 23 | 4 | 4 | 8 | 27 |
| Dioscoreaceae | 1 | 1 | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . |
| Dipsacaceae | 6 | 24 | 7 | 1 | 2 | . | 3 | 2 | 2 | 2 | . | . | 5 | . | . | . | . |
| Droseraceae | 1 | 1 | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . |
| Elatinaceae | 1 | 3 | . | . | . | . | . | . | . | . | . | 1 | 1 | 1 | . | . | . |
| Ephedraceae | 1 | 5 | . | 1 | . | . | . | 1 | 3 | . | . | . | . | . | . | . | . |
| Ericaceae | 3 | 9 | . | . | 2 | . | 3 | . | 2 | . | . | 1 | . | . | 1 | . | . |
| Euphorbiaceae | 5 | 62 | 13 | 4 | 7 | 1 | 9 | 4 | 9 | . | 4 | 2 | 7 | . | . | 1 | 2 |
| Fagaceae | 2 | 8 | 1 | . | 2 | . | 1 | 3 | . | . | . | 1 | . | . | . | . | . |
| Frankeniaceae | 1 | 6 | 1 | 2 | . | . | . | 1 | 1 | . | . | 1 | . | . | . | . | . |
| Gentianaceae | 6 | 16 | 3 | . | . | . | . | . | 7 | . | . | 1 | 2 | 1 | 2 | . | . |
| Geraniaceae | 2 | 47 | 17 | . | 4 | . | 3 | 2 | 12 | . | 1 | 1 | 7 | . | . | . | . |
| Gramineae | 114 | 338 | 42 | 10 | 20 | . | 21 | 12 | 89 | . | 14 | 8 | 51 | 20 | 1 | 24 | 32 |
| Grossulariaceae | 1 | 3 | . | . | . | . | . | . | . | . | . | . | 3 | . | . | . | . |
| Haloragidaceae | 2 | 4 | . | . | . | . | . | . | . | . | . | . | 1 | . | 2 | . | 1 |
| Hippuridaceae | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Hydrocharitaceae | 3 | 3 | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | 2 |
| Hypericaceae | 1 | 24 | 2 | . | 2 | 1 | 2 | 2 | 10 | . | . | 1 | 3 | 1 | . | . | . |
| Illecebraceae | 1 | 1 | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . |
| Iridaceae | 5 | 32 | 9 | . | 8 | . | 3 | . | 8 | . | 3 | 1 | . | . | . | . | . |

TABLE 3. *Continued.*

| Family | Gen. | Sp. | End. | N.A. | I.-M. | Mac. | W.-Med. | E.-Med. | Med. | I.-T. | S.-S. | Atl. | E.&E. | Pt. | Cb. | Trop. | Oth. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Juglandaceae | 1 | 1 | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . |
| Juncaceae | 2 | 29 | 1 | . | 1 | . | 2 | . | 5 | . | . | 1 | 9 | 4 | 1 | 1 | 4 |
| Juncaginaceae | 1 | 4 | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | 3 |
| Labiatae | 34 | 222 | 99 | 8 | 32 | . | 19 | 4 | 33 | . | 1 | . | 21 | 2 | 1 | . | 2 |
| Lauraceae | 1 | 1 | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . |
| Leguminosae | 49 | 432 | 105 | 4 | 61 | 3 | 43 | 21 | 146 | 3 | 10 | 3 | 31 | 2 | . | . | . |
| Lemnaceae | 3 | 5 | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | 4 |
| Lentibulariaceae | 2 | 5 | . | . | . | . | . | . | . | . | . | 1 | 2 | 1 | . | 1 | . |
| Liliaceae | 24 | 113 | 25 | 1 | 9 | 1 | 15 | 8 | 37 | 2 | 1 | 1 | 12 | 1 | . | . | . |
| Linaceae | 3 | 18 | 7 | . | 1 | . | 3 | 1 | 4 | . | . | . | 2 | . | . | 1 | . |
| Loranthaceae | 2 | 3 | . | . | . | . | . | . | 1 | . | . | . | 1 | 1 | . | . | . |
| Lythraceae | 2 | 8 | . | . | 1 | . | . | . | 4 | . | . | . | 1 | . | . | . | 2 |
| Malvaceae | 6 | 32 | 6 | . | 5 | . | 1 | 2 | 11 | . | 1 | 1 | 4 | . | . | . | 1 |
| Menyanthaceae | 1 | 1 | . | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . |
| Monotropaceae | 1 | 1 | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . |
| Moraceae | 1 | 1 | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . |
| Myrtaceae | 1 | 1 | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . |
| Najadaceae | 1 | 5 | 1 | . | . | . | . | . | . | . | . | . | . | . | . | 1 | 3 |
| Nyctaginaceae | 2 | 2 | 1 | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . |
| Nymphaeaceae | 2 | 2 | . | . | . | . | . | . | . | . | . | . | 2 | . | . | . | . |
| Oleaceae | 5 | 6 | . | . | . | . | . | . | 4 | . | . | . | 2 | . | . | . | . |
| Onagraceae | 6 | 14 | 3 | . | . | . | . | . | 1 | . | . | 1 | 1 | 2 | 1 | 2 | 3 |
| Orchidaceae | 13 | 54 | 5 | . | . | . | 5 | . | 20 | . | . | . | 24 | . | . | . | . |
| Orobanchaceae | 2 | 40 | 9 | 1 | 5 | . | 3 | 1 | 8 | . | 2 | 1 | 9 | . | . | 1 | 1 |
| Oxalidaceae | 1 | 3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 3 |
| Paeoniaceae | 1 | 1 | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . |
| Palmae | 2 | 2 | . | . | . | . | 1 | . | . | . | 1 | . | . | . | . | . | . |
| Papaveraceae | 11 | 52 | 11 | 1 | 11 | . | 3 | 4 | 9 | . | . | . | 10 | . | . | 1 | 2 |
| Parnassiaceae | 1 | 1 | . | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . |
| Phytolaccaceae | 1 | 2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2 |

TABLE 3. *Continued.*

| Family | Gen. | Sp. | End. | N.A. | I.-M. | Mac. | W.-Med. | E.-Med. | Med. | I.-T. | S.-S. | Atl. | E.&E. | Pt. | Cb. | Trop. | Oth. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Pinaceae | 3 | 6 | 1 | 1 | 1 | . | . | . | 3 | . | . | . | . | . | . | . | . |
| Plantaginaceae | 2 | 23 | 4 | 1 | . | . | 3 | . | 8 | . | 1 | . | 5 | . | 1 | . | . |
| Plumbaginaceae | 5 | 46 | 17 | 3 | 5 | . | 6 | . | 6 | 1 | 3 | 5 | . | . | . | . | . |
| Polygalaceae | 1 | 7 | 3 | . | 1 | . | 1 | . | 2 | . | . | . | . | . | . | . | . |
| Polygonaceae | 3 | 36 | 5 | 1 | . | . | 1 | . | 5 | . | 3 | 1 | 6 | 1 | 1 | 1 | 11 |
| Portulacaceae | 2 | 2 | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | 1 |
| Posidoniaceae | 1 | 1 | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . |
| Potamogetonaceae | 1 | 12 | . | . | . | . | . | . | . | . | . | . | 1 | 3 | . | . | 8 |
| Primulaceae | 9 | 16 | 2 | . | . | . | 1 | 1 | 3 | . | . | 2 | 5 | . | 2 | . | . |
| Punicaceae | 1 | 1 | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . |
| Pyrolaceae | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Rafflesiaceae | 1 | 1 | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . |
| Ranunculaceae | 13 | 64 | 10 | . | 2 | . | 6 | 2 | 14 | 1 | . | 2 | 19 | 5 | . | . | 3 |
| Resedaceae | 4 | 25 | 11 | . | 3 | . | 1 | . | 1 | 3 | 1 | . | . | . | 3 | 1 | 1 |
| Rhamnaceae | 3 | 8 | . | . | . | . | 2 | . | 4 | . | . | . | 2 | . | . | . | . |
| Rosaceae | 19 | 60 | 6 | . | 6 | . | 3 | 2 | 9 | 1 | 1 | 1 | 28 | 1 | 2 | . | . |
| Rubiaceae | 9 | 50 | 8 | 4 | 5 | . | 3 | 1 | 17 | . | . | 1 | 9 | 1 | . | 1 | . |
| Ruppiaceae | 1 | 2 | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | 1 |
| Rutaceae | 2 | 4 | 1 | . | 1 | . | . | . | 2 | . | . | . | . | . | . | . | . |
| Salicaceae | 2 | 10 | . | . | . | . | . | . | 1 | 1 | . | . | 8 | . | . | . | . |
| Sambucaceae | 1 | 2 | . | . | . | . | . | . | . | . | . | . | 2 | . | . | . | . |
| Santalaceae | 2 | 6 | 2 | . | 1 | . | . | . | 3 | . | . | . | . | . | . | . | . |
| Sapindaceae | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Sapotaceae | 1 | 1 | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Saxifragaceae | 2 | 18 | 7 | . | 4 | . | 2 | 3 | . | . | . | . | 2 | . | . | . | . |
| Scrophulariaceae | 18 | 145 | 50 | 9 | 21 | . | 11 | 22 | . | . | 5 | 3 | 16 | 2 | 4 | 1 | . |
| Selaginaceae | 1 | 3 | 2 | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . |
| Solanaceae | 9 | 18 | 1 | . | 4 | . | . | 1 | 3 | . | 1 | . | 3 | . | . | 1 | 4 |
| Sparganiaceae | 1 | 1 | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . |
| Tamaricaceae | 2 | 10 | . | 2 | 1 | . | 1 | 1 | . | . | 3 | 1 | . | 1 | . | . | . |
| Taxaceae | 1 | 1 | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . |
| Theligonaceae | 1 | 1 | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . |

TABLE 3. *Continued.*

| Family | Gen. | Sp. | End. | N.A. | I.-M. | Mac. | W.-Med. | E.-Med. | Med. | I.-T. | S.-S. | Atl. | E.&E. | Pt. | Cb. | Trop. | Oth. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Thymelaeaceae | 2 | 17 | 4 | 2 | 4 | . | . | . | 4 | . | 1 | . | 2 | . | . | . | . |
| Trapaceae | 1 | 2 | . | . | . | . | . | . | . | . | . | . | . | 1 | . | 1 | . |
| Typhaceae | 1 | 3 | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | 2 |
| Ulmaceae | 2 | 2 | . | . | . | . | . | . | 1 | . | . | . | 1 | . | . | . | . |
| Umbelliferae | 61 | 183 | 53 | 9 | 21 | 5 | 12 | 7 | 38 | 2 | 2 | 5 | 28 | 1 | . | . | . |
| Urticaceae | 3 | 8 | . | . | 1 | . | . | 1 | 3 | . | 1 | . | 2 | . | . | . | . |
| Vahliaceae | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| Valerianaceae | 4 | 26 | 4 | 2 | 3 | . | 2 | 2 | 10 | . | . | 1 | 2 | . | . | . | . |
| Verbenaceae | 3 | 5 | . | . | . | . | . | . | 2 | . | . | . | . | . | . | . | 3 |
| Violaceae | 1 | 10 | 4 | . | . | . | . | . | 2 | . | . | . | 3 | . | 1 | . | . |
| Vitaceae | 1 | 1 | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . |
| Zannichelliaceae | 2 | 2 | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | 1 |
| Zosteraceae | 1 | 2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2 |
| Zygophyllaceae | 6 | 10 | 3 | . | . | 1 | 1 | . | . | 2 | 2 | . | . | . | . | 1 | . |
| TOTALS | 916 | 4034 | 1038 | 78 | 408 | 27 | 321 | 160 | 873 | 33 | 122 | 63 | 528 | 73 | 40 | 56 | 214 |
| PERCENTAGES | | | 25.76 | 1.93 | 10.13 | 0.57 | 7.97 | 3.97 | 21.68 | 0.81 | 3.00 | 1.56 | 13.11 | 1.83 | 0.99 | 1.36 | 5.31 |

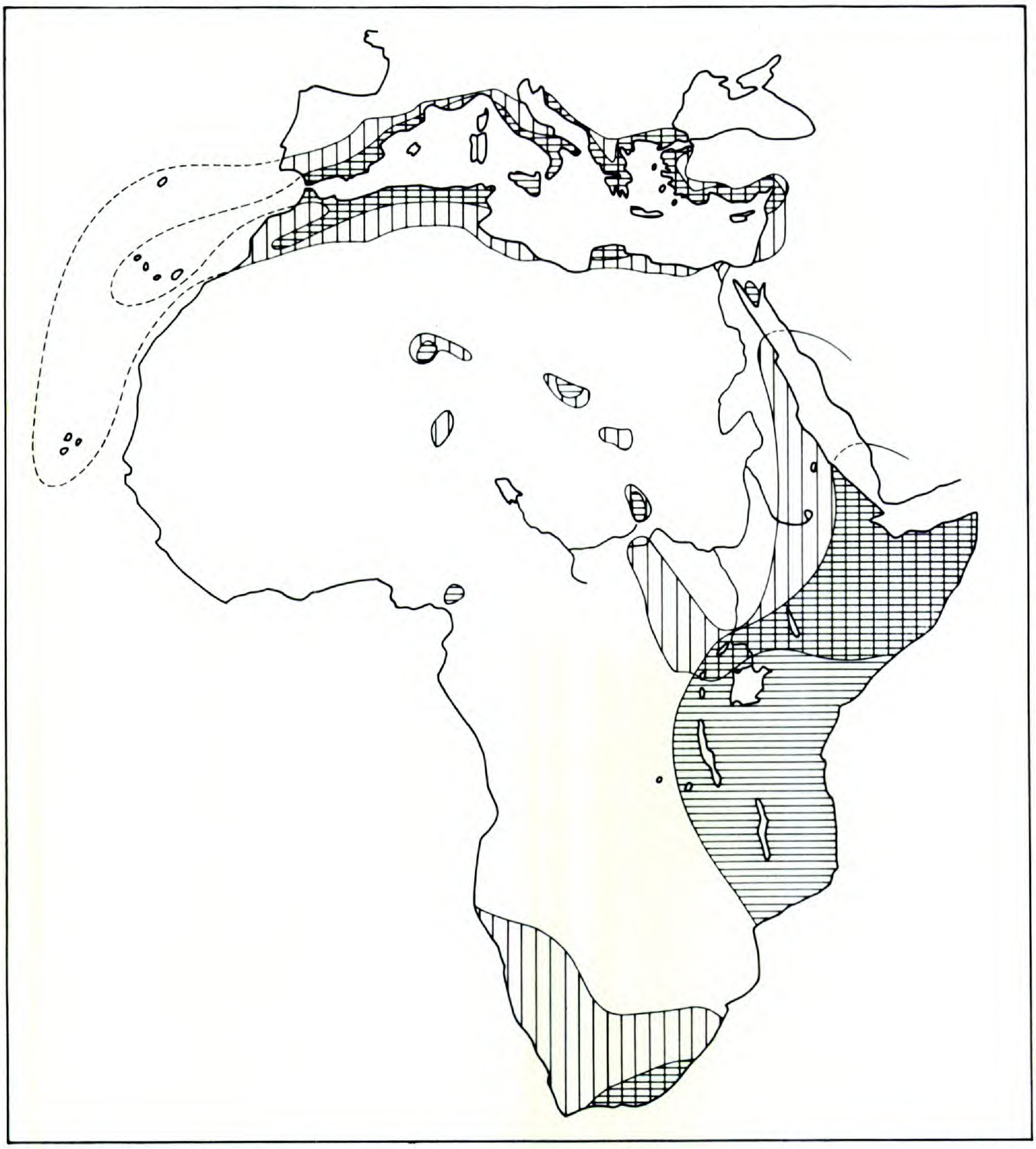

FIGURE 3. Distribution of *Hyparrhenia hirta* (vertical lines) and *Andropogon distachyus* (horizontal lines).

*Raffenaldia*, *Hemicrambe*, *Cordylocarpus*, *Fezia*, *Kremeriella*, *Muricaria*, *Crambella*, *Otocarpus*, *Ceratocnemum*, *Rhytidocarpus*, and *Psychine*; 4 to the Compositae: *Fontquera*, *Anvilleina*, *Lifago*, and *Mecomiscus*; 3 to the Umbelliferae: *Sclerosiadium*, *Pachyctenium*, and *Balansaea*; 4 to the Leguminosae: *Hesperolaburnum*, *Argyrocytisus*, *Lyauteya*, and *Benedictella*; 2 to the Gramineae: *Libyella* and *Agropyropsis*; to the Labiateae: *Saccocalyx* and *Pitardia*; and to the Chenopodiaceae: *Oreobliton* and *Traganopsis*. Finally there is an endemic genus in the following families: Liliaceae (*Battandiera*), Amaryllidaceae (*Hannonia*), Sapotaceae (*Argania*), and Campanulaceae (*Feeria*).

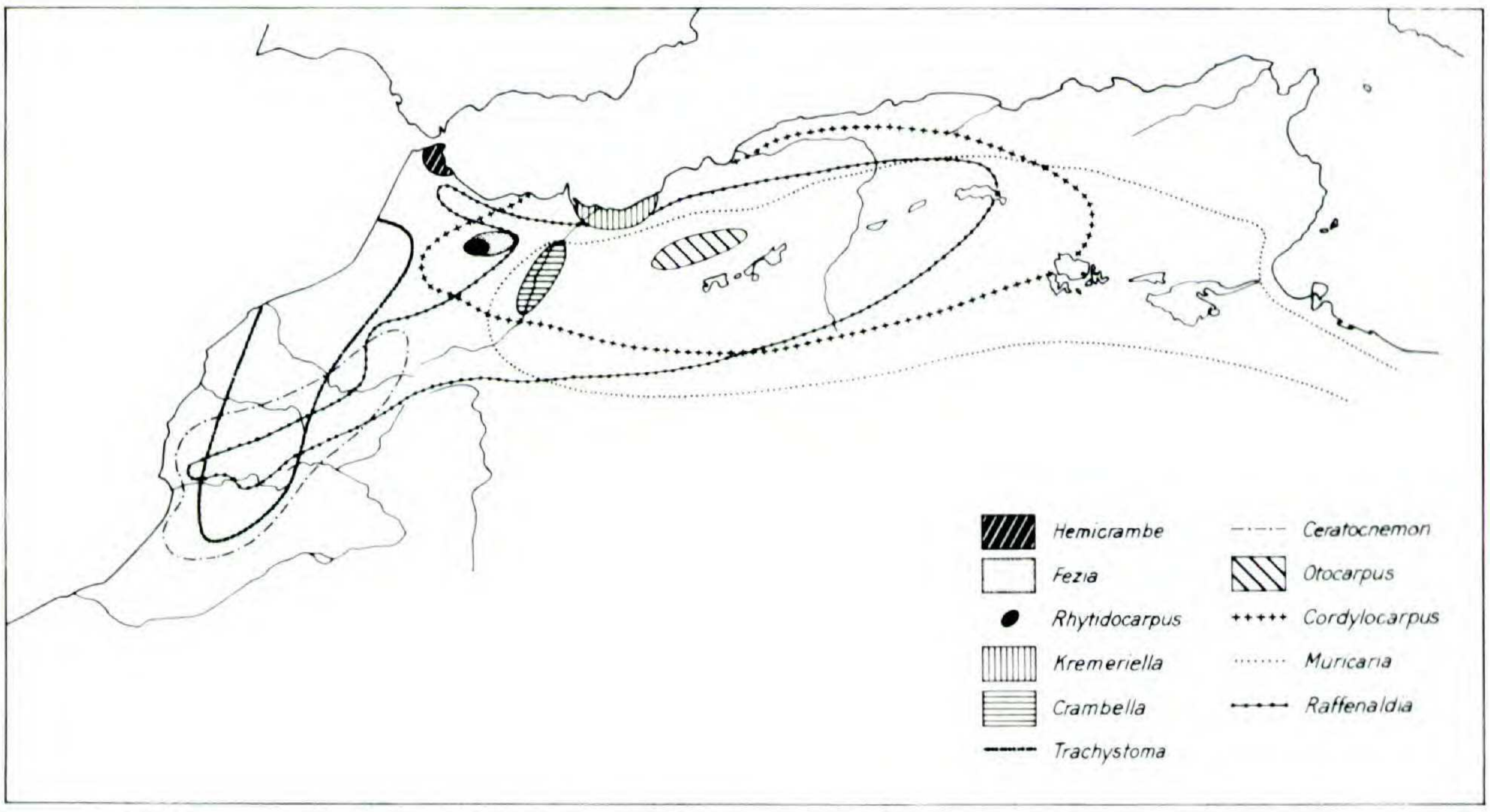


FIGURE 4. Distribution of endemic genera of Cruciferae in Mediterranean North Africa. *Psychine* occurs nearly throughout Mediterranean North Africa.

Most of these genera are monospecific and have a restricted distribution (cf. Fig. 4). However, *Trachystoma* has three species and *Raffenaldia*, *Pitardia* and *Mechomiscus* have two species.

Certainly, the most remarkable characteristic is the real generic proliferation which appears in the Maghreb in the Cruciferae.

Among the other genera, some are certainly related to other North African or Mediterranean genera; others, on the other hand, represent paleoendemic elements. Among the former are *Anvilleina*, *Lifago*, *Libyella*, *Agropyropsis*, *Saccocalyx*, *Traganopsis*, *Battandiera*, whose links with the genera *Anvillea*, *Filago*, *Mibora*, *Agropyron*, *Thymus*, *Traganum* and *Ornithogalum* are evident.

## II.3.2—*Specific Endemism*

Of the some 925 genera inventoried in this work for Mediterranean Africa, about 330, or 30%, have endemic species. It would be too lengthy to enumerate these species here, but it is nevertheless interesting to learn something about the genera having the largest number of endemic species. I have not gone beyond four endemic species per genus: 48: *Silene*; 34: *Centaurea*, 25: *Teucrium*; 23: *Linaria*; 18: *Astragalus*, *Thymus*; 16: *Ononis*, *Euphorbia*; 15: *Erodium*; 14: *Limonium*; 13: *Bupleurum*, *Leucanthemum*, *Crepis*; 12: *Sedum*, *Genista*, *Campanula*; 11: *Reseda*, *Echium*, *Marrubium*, *Stachys*, *Atractylis*; 10: *Vicia*, *Celsia*; 9: *Sideritis*, *Carthamus*, *Carduncellus*; 8: *Romulea*, *Helianthemum*, *Galium*, *Orobanche*, *Anacyclus*, *Chrysanthemum*, *Senecio*; 7: *Fumaria*, *Arabis*, *Saxifraga*, *Adenocarpus*, *Cytisus* (sensu lato), *Lotus*, *Linum*, *Convolvulus*, *Salvia*, *Micromeria*, *Onopordum*, *Leontodon*, *Taraxacum*; 6: *Festuca*, *Scilla*, *Allium*, *Rumex*, *Spergularia*, *Ranunculus*, *Diplotaxis*, *Alyssum*, *Hedysarum*, *Lavatera*, *Eryngium*, *Carum, Odontites, Phagnalon, Andryala*; 5: *Arenaria, Buffonia, Lathyrus, Daucus, Valerianella, Scabiosa, Verbascum, Scrophularia, Plantago, Armeria, Thymelaea, Pulicaria, Filago, Anthemis, Cirsium, Launaea*; 4: *Avena, Cynosurus, Atriplex, Delphinium, Brassica, Potentilla, Viola, Bunium, Pituranthos, Ferula, Lavandula, Calamintha, Origanum, Evax, Calendula, Artemisia, Hypochoeris, Picris, Hieracium.*

Without going into a biogeographical interpretation, it is nevertheless appropriate to point out that nearly all of these genera are unquestionably of Mediterranean origin; the only notable exceptions are *Saxifraga, Festuca, Ranunculus, Avena, Potentilla, Viola, Cirsium* and *Hieracium*, more generally Eurasian or Holarctic, *Artemisia* and *Atriplex*, better developed in the Irano-Turanian Region, and *Pituranthos*, of Saharan origin.

### II.3.3—*Biogeographical Significance of Endemic Taxa*

It is impossible to study here in detail the biogeographical significance of the 1,037 endemic species inventoried in Mediterranean Africa; it is nevertheless interesting to clarify at least some points.

II.3.3.1—*Endemics of Mediterranean Origin.*—These represent more than 80% of the total. Among these, more than a third are related to genera essentially circum-Mediterranean, the principal ones being: *Asphodelus, Scilla, Brassica, Diplotaxis, Arabis, Reseda, Sedum, Ononis, Trifolium, Lavatera, Ferula, Cyclamen, Globularia, Teucrium, Salvia, Sideritis, Stachys, Campanula, Evax, Anacyclus, Anthemis, Chrysanthemum*, and *Centaurea.*

The genera more specifically Western Mediterranean are perhaps even better represented by: *Catapodium, Romulea, Spergularia, Silene, Hedysarum, Helianthemum, Erodium, Eryngium, Bupleurum, Echium, Linaria, Odontites, Solenanthus, Armeria, Limonium, Lavandula, Thymus, Filago, Calendula, Atractylis, Carthamus*, and *Carduncellus.*

Among the genera of Ibero-Mauritanian origin, endemics are present in *Leucojum, Vagaria, Rupicapnos, Adenocarpus, Lafuentia, Brachyapium.*

Inversely, the endemics belonging to the genera *Bellevalia, Tunica, Astragalus, Cicer, Pterocephalus, Rindera, Micromeria* are more generally of Eastern Mediterranean origin.

Since a biogeographical and taxonomic interpretation is already nearly complete, (Quézel, 1957, 1964a), we shall not discuss it at length. However, we would still like to emphasize a certain number of points.

II.3.3.2—*Endemics of North African Origin.*—Along with the endemic genera mentioned above, one should point out the existence of endemic sections in the genera *Agropyron* (*Goulardiopsis* by *A. embergeri*), *Draba* (*Helicodraba* by *D. hederifolia* and *Acrodraba* by *D. oreadum*), *Phagnalon* (*Gnaphaliopsis* by *P. helichrysoides, P. platyphyllum, P. embergeri* and *P. iminouakense*), *Cyclamen* (*Dodecatheoides* by *C. rohlfsianum*).

Some genera also have some very distinctive species in North Africa. Such is the case for the hardy *Cynosurus* (*C. peltieri, C. balansae*, and *C. junceus*), for the shrubby *Polygala* (*P. balansae, P. webbiana*, and *P. munbyana*), the

*Adenocarpus* with umbelliform inflorescences (*A. umbellatus*, *A. faurei*, and *A. segonei*) and also the *Buffonia perennes* group.

II.3.3.3—*The Mountain Endemics.*—The North African mountains (Quézel, 1957) contain one of the most remarkable concentrations of endemic taxa in North Africa; in fact, there are about 170 on the high Moroccan Atlas. A large number of these endemics belong to genera or to groups of species of orophytes which are circum-Mediterranean, or even Mesogean. These emphasize the strict affinities existing in the original plant population of the mountains of the Mediterranean periphery. A few examples are (Fig. 5) the representatives of the genera *Cedrus* and *Abies*, as well as *Cicer atlanticum*, a very exact vicariant of *C. incisum* of Greece and of the Near East, and of *C. minutum* of Ebourouz. There are many other examples in the genera *Minuartia*, *Silene*, *Potentilla*, *Astragalus*, *Viola*, *Hypericum*, *Sideritis*, *Marrubium*, *Veronica*, *Asperula*, *Pterocephalus*, *Rindera*, *Campanula*, and *Leuzea*.

II.3.3.4—*Endemics of Northern Origin (in the broad sense).*—Although these are not very numerous, they are of some interest. Even though the migration to North Africa of species of northern origin generally appears recent and, for the most part, concomitant with glaciations (the nearly total absence of specific endemism proves it clearly), some noteworthy exceptions point to the possibility of a much older migration. Thus it is that the genus *Gentiana* is represented on the high Atlas by two endemic species, one of which (*G. tornezyana*) is the type of the section *Pseudotricha*, and the other (*G. atlantica*) belongs to an orophilous southern European lineage absent, however, from the Alps.

Other examples are the following: *Agrostis atlantica*, vicariant of *A. rupestris*; *Luzula atlantica*, related to *L. graeca*; representatives of the genera *Erigeron* and *Gnaphalium*, also related to European or Anatolian species. Still in the Atlas, *Aster pujosii*, vicariant of *A. amellus* and *A. willkommii*, can be linked to the element of Sarmatic origin. Some endemics of northern origin are found in North Africa, especially on the eastern Algerian coast at low altitudes. Their presence there seems to be very old. Such is the case for *Digitalis atlantica*, *Pedicularis numidica*, *Lysimachia cousiniana*, *Epimedium parralderianum*, *Epilobium numidicum*, *Galium numidicum*, related specifically and respectively to *D. ambigua*, *P. silvatica*, *L. nemorum*, *E. pubigenum*, *E. parviflorum* and *G. mollugo*.

*Coronilla atlantica* and *Doronicum atlanticum*, as well as the *Teucrium* endemics of the *Scorodonia* section, have a comparable significance, but a wider distribution.

II.3.3.5—*Endemics of Irano-Turanian and Saharo-Arabian Origin.*—These endemics are not numerous. However, endemics of Irano-Turanian origin are, probably, *Zygophyllum cornutum*, *Anabasis prostrata*, as well as various representatives of the genus *Artemisia* (particularly *A. atlantica*, *A. mesatlantica*, and *A. ifranensis*) whose affinities with *A. herba-alba* are evident. The same applies to the genus *Hohenackeria* (*H. polyodon*).

The only endemic species of Saharan origin found within the limits of the Mediterranean region appears to be *Fagonia harpago* of the southern face of the Anti-Atlas.

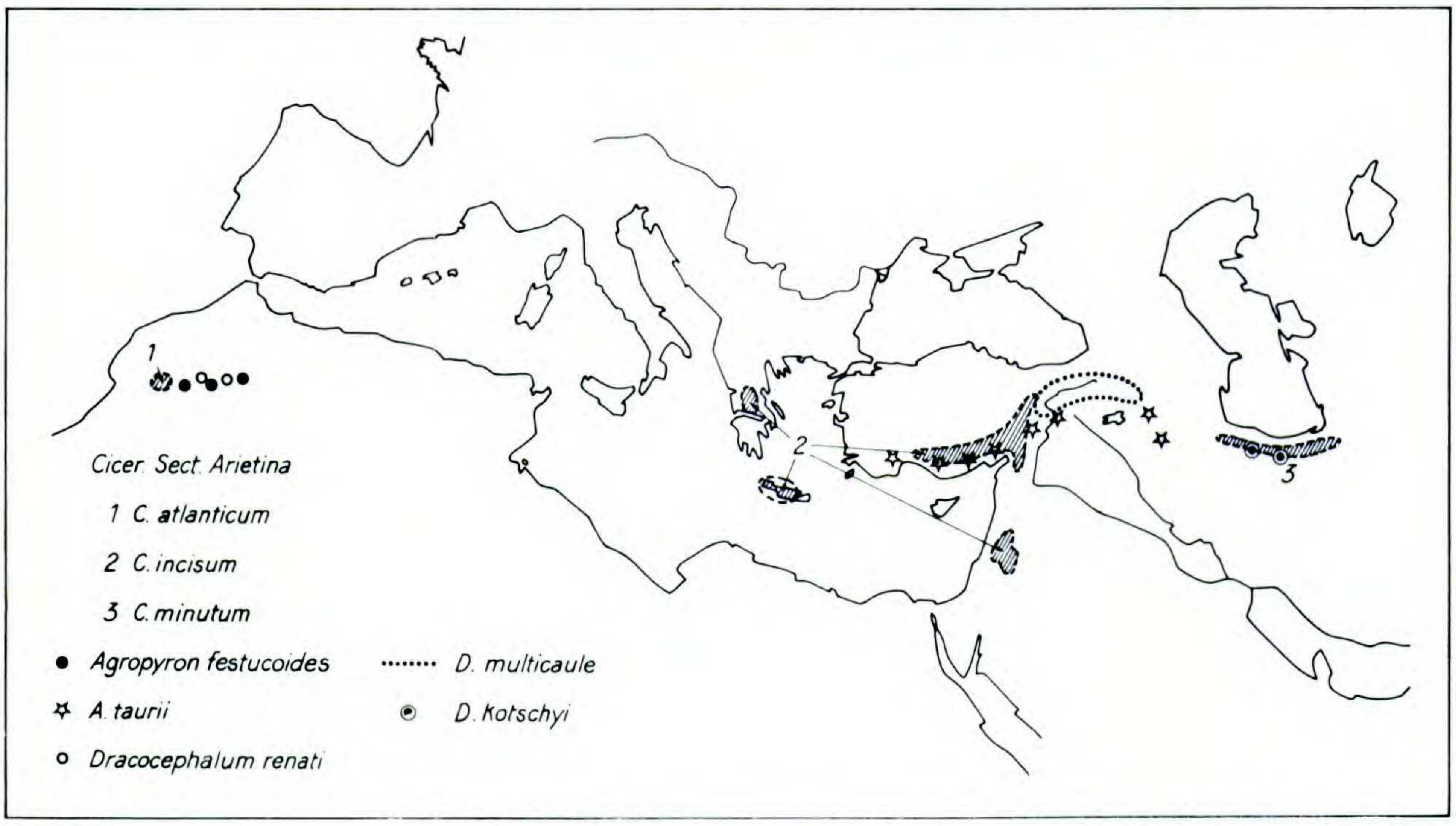


FIGURE 5. Distribution of North African mountain endemics.

II.3.3.6—*Endemics of Tropical Origin.*—Although not numerous in Mediterranean Africa (about 15), these are nevertheless noteworthy from several points of view. First, it is relevant to note that the largest number of them is found in southern Morocco, especially in the Macaronesian section of this country. In fact, most also have vicariants in the Canaries or could be integrated, if necessary, into the Macaronesian element. Specific examples are *Acacia gummifera, Commelina rupestris, Boerhaavia maroccana, Kalanchoe faustii, Leptochloa ginae,* and *Pentzia hesperidum,* all the only representatives of these genera in Mediterranean Africa.

Among the other endemic species of tropical African origin that are widespread in North Africa are two representatives of the genus *Hertia* (*H. cheirifolia* and *H. maroccana*), and of the genus *Caralluma* (*C. hesperidum* and *C. joannis*), as well as *Polycarpaea akkensis, Andrachne maroccana,* and *Cleome amblyocarpa.*

The genera *Lotononis* (with 3 endemic species in Morocco) and *Argyrolobium* (2 species) are also of tropical African origin. *Trichodesma calcaratum* and *Withania adpressa* are found in the Sahara, but are otherwise found mainly in Mediterranean Africa.

The relatively large representation of endemics of tropical origin in southern Morocco is well known, but merits attention. Indeed, their presence is certainly old in this zone and points to the possibilty of floristic exchanges between the Mediterranean and tropical regions, certainly since the Tertiary and probably even before the Saharan aridification (cf. below). The continued presence of these species, often quite rare as well, has been conditioned by the local climate and essentially by the high degree of atmospheric humidity. It should be pointed out that the coast of the Red Sea must have played an analogous role even though endemism there is scarcely perceptible for tropical taxa which, in any case, are not found in the Mediterranean region.

II.3.3.7—*Endemics of Macaronesian Origin.*—Macaronesian endemics occur of course, mainly in the Macaronesian Moroccan region whose essential physiognomic element is *Argania spinosa.* However, this tree, as well as several other species, spread more or less widely into the Mediterranean region, and notably into the oceanic Sahara. The endemic elements most representative are *Euphorbia echinus, Senecio antheuphorbium, Bubonium imbricatum, Aizoon theurkauffii, Limonium beaumierianum, L. tuberculatum, Limoniastrum ifniense, Lotus pseudo-creticus, L. simonae,* and *Frankenia chevallieri.*

In Algeria, at Bejaïa, *Bupleurum plantagineum* also appears to belong to this group. In fact it is close to *B. salicifolium* of the Canaries and of Madeira, but also to *B. dumosum* of the Ida or Tanana of western Morocco.

### II.3.4—*The Geographical Aspect of Endemism in Mediterranean Africa*

It is evident that the Maghreb alone is the basic reservoir for the endemic species. In fact, of some 1,037 species cited, almost a thousand are found there.

No estimate is made here of the number of endemic species in each of the countries of the Maghreb since this does not correspond to any geographical reality. Nevertheless, this count has been made for Algeria (Quézel, 1964b), where about 250 endemic species exist. Recently Lecompte-Barbet (1975) made this study for Morocco, but she clearly gives too broad a meaning to this term at the taxonomic level (she includes subspecies in her totals) as well as at the geographical level. Therefore it is difficult to estimate from these results what the actual specific endemism of Morocco is; numbers on the order of 600–650 are likely.

A very special case which deserves attention is that of the Cyrenaic Mediterranean, which has very distinctive characteristics and a certain influence of eastern Mediterranean elements in the makeup of its endemic ancestry. It is difficult to calculate the exact number, but it is probably more than 40. Among those unquestionably having elements of eastern Mediterranean origin are: *Bellevalia cyrenaica, Allium* spp., *Arum cyrenaicum, Crocus boulosii, Ornithogalum barba-caprae, Athamantha della-cellae, Tunica daveana, T. marmarica, Astragalus cyrenaicus, A. taubertianus, Origanum cyrenaicum, Micromeria guichardii, M. fortii, Nepeta cyrenaica, Teucrium barbeyanum, T. davaeanum,* and *Arbutus pavarii.*

Other species are more typically of circum-Mediterranean origin. These are: *Avena beguinotiana, Cynosurus junceus, Orchis cyrenaica, Thesium erythronicum, Silene daveana, S. marmarica, Reseda odorata, R. pampaniniana, Sedum mirum, S. bracteatum, Medicago cyrenaica, Convolvulus mairei, Plantago phaeostoma, Onopordum cyrenaicum, Libyella cyrenaica, Cyclamen rohlfsianum, Viola scorpiuroides,* and *Pachyctenium mirabile.*

Egypt, on the contrary (excluding Sinai), has only a small number of endemic species in its Mediterranean portion. Noted may be: *Tunica compressa, Lotus polyphyllus, Ebenus armitagei,* and *Ferula marmarica.*

## III—Saharan Africa

The vast desert zone stretching between Mediterranean Africa on the north and tropical Africa on the south, and for which we have previously indicated the boundaries, which is truly quite artificial, occupies approximately 7,000,000 $km^2$.

In this enormous territory, in spite of an usually extremely hostile climate, developed a flora of great importance, which is especially prevalent in the wettest areas: the northern and southern borders, the ocean shores, and in particular the mountain massifs. This flora presents many problems of biological and geobotanical significance, problems essentially related to the climatic history and especially to the recent climatic history of this area, where next to the eremitic autochthonous elements, an often significant number of Mediterranean and tropical elements appears. In fact, even if some of the eremetic elements are truly from the Sahara (in the actual sense of the term), others belong to the old African xerophytic flora usually called the "Rand Flora."

For all these reasons, the analysis of the flora presently occupying the Sahara is particularly delicate, but also very interesting and instructive!

### III.1—the families

#### III.1.1—*Generic and Specific Richness* (Table 5)

For the entire Saharan region about 104 families of phanerogamic plants have been divided into several categories; for the vascular cryptogams about 10.

Concerning the generic representation, the hierarchy is as follows: 2 families contain more than 50 genera (Compositae 80 and Gramineae 74), 4 more than 20 (Cruciferae 44, Leguminosae 30, Chenopodiaceae 23, Caryophyllaceae 22), 7 more than 10 (Umbelliferae 18, Boraginaceae 17, Labiatae and Scrophulariaceae 16, Aizoaceae, Asclepiadaceae and Liliaceae 11). Fourteen families possess between 6 and 10 genera (Convolvulaceae, Cucurbitaceae, Euphorbiaceae and Rubiaceae 9, Cyperaceae, Malvaceae and Zygophyllaceae 8, Acanthaceae and Capparaceae 7, Amaranthaceae, Papaveraceae, Polygonaceae, Solanaceae and Verbenaceae 6). Thirty-seven families contain from 2 to 5 genera, and 37 are monospecific in the Saharan area.

In the vascular cryptogams, all of the Filicales embrace 11 genera, the other families (4) are represented by a single genus.

In species richness, only 3 families surpass 100 (Gramineae 203, Compositae 164, Leguminosae 154), 3 surpass the 50 mark (Cruciferae 73, Chenopodiaceae 64, Caryophyllaceae 73), and 14 families possess between 20 and 49 species (Scrophulariaceae 49, Cyperaceae 46, Boraginaceae and Zygophyllaceae 43, Euphorbiaceae 40, Malvaceae 38, Labiatae 36, Umbelliferae 35, Convolvulaceae 34, Aizoaceae 25, Asclepiadaceae and Capparaceae 23, Rubiaceae 22, Solanaceae 21). Fifteen families have between 10 and 19 species (Liliaceae 19, Polygonaceae 18, Geraniaceae, Papaveraceae and Tamaricaceae 15, Amaranthaceae and Cucurbitaceae 14, Cistaceae, Plantaginaceae and Resedaceae 13, Plumbaginaceae 12, Ranunculaceae 11, Acanthaceae, Juncaceae and Potamogetonaceae 10). In addition 21 families possess from 5 to 9 species. Four species are found in 3 families, 3 in 7, and 2 in 15. Finally, 21 families are represented in the Sahara by only a single species.

### III.1.2—*Biogeographical Significance at the Family Level*

Let me emphasize immediately, that contrary to what happened in Mediterranean Africa, the families offer very diverse biogeographical significance. Later on I will return to this question which is one of the fundamental aspects of the Saharan flora, but it is, however, interesting to emphasize that the tropical element is in the majority in a large number of families. Particularly to be noted are the following: Acanthaceae, Aizoaceae, Amaranthaceae, Asclepiadaceae, Burseraceae, Capparaceae, Commelinaceae, Convolvulaceae, Cucurbitaceae, Elatinaceae, Euphorbiaceae, Leguminosae, Lythraceae, Malvaceae, Menispermaceae, Moraceae, Nyctaginaceae, Pedaliaceae, Sapindaceae, Solanaceae, Sterculiaceae, Tiliaceae, Vahliaceae, Verbenaceae, and Vitaceae. Such is still the case for the Avicenniaceae, Balanitaceae, Combretaceae, Ebenaceae, Moringaceae, Rhizophoraceae, and Salvadoraceae, all represented by a single species in the Sahara.

The Saharan element (sensu lato) dominates in the Boraginaceae, Chenopodiaceae, Compositae, Cruciferae, Frankeniaceae, Plumbaginaceae, Resedaceae, Tamaricaceae, and Zygophyllaceae.

The Mediterranean element dominates in the Araceae, Caryophyllaceae, Ephedraceae, Geraniaceae, Labiatae, Orobanchaceae, Papaveraceae, Plantaginaceae, Rhamnaceae, Santalaceae, and Umbelliferae.

Finally, it may be noted that Polygonaceae, Ranunculaceae, and Salicaceae predominately exhibit the Irano-Turanian element, although this phenomenon is not particularly significant except perhaps for the Polygonaceae. With the Juncaceae, Najadaceae, and Potamogetonaceae, the cosmopolitan species or those with a very vast area of distribution are dominant.

### III.1.3—*Endemic Richness at the Family Level*

One must emphasize at the beginning the considerable impoverishment in endemic species that can be observed in the Sahara in comparison to Mediterranean Africa. The total percentage of endemics is no more than 11.6%, in contrast to 25.7% in Mediterranean Africa.

One single family shows more than 20 endemic species (Leguminosae 21) and 6 more than 10 (Gramineae 19, Caryophyllaceae, Compositae and Umbelliferae 13, Cruciferae 12, and Zygophyllaceae 10). Three show from 5 to 10 (Scrophulariaceae 7, Euphorbiaceae and Plumbaginaceae 5). There are 4 endemic species in the Asclepiadaceae, Boraginaceae, Cistaceae, Labiatae and Rubiaceae, 3 in the Aizoaceae, Dipsacaceae, Ephedraceae, Liliaceae, Papaveraceae and Polygonaceae, and 2 in the Chenopodiaceae, Convolvulaceae, Cyperaceae, Gentianaceae, Hypericaceae, and Resedaceae. Finally, Apocynaceae, Crassulaceae, Cupressaceae, Elatinaceae, Frankeniaceae, Geraniaceae, Malvaceae, Moraceae, Myrtaceae, Nyctaginaceae, Oleaceae, Onagraceae, Plantaginaceae,

TABLE 4. Distribution of the total number of species in Saharan Africa into its biogeographical subdivisions.

| Subdivision | Number | Percentage % |
|---|---|---|
| Number of genera | 617 | |
| Number of species | 1,620 | |
| Endemics (sensu lato) | 190 | 11.6 |
| Saharo-Arabian | 359 | 22.7 |
| Irano-Turanian | 75 | 4.5 |
| Mediterranean (sensu lato) | 344 | 21.2 |
| Tropical (sensu lato) | 524 | 32.3 |
| Cosmopolitan or plurilocal and others | 126 | 7.7 |

Polygalaceae, Primulaceae, Ranunculaceae, Rosaceae, Solanaceae, Tamaricaceae, and Verbenaceae possess only one.

It is notable that in the Sahara, 51 families do not possess endemic species, estimated at a rough guess to be half of the families present.

### III.1.4—*The Global Biogeographical Spectrum*

In order not to excessively complicate an often controversial question, I only consider the Saharo-Arabian, Irano-Turanian, and Mediterranean elements, and some of tropical origin, in Table 4 and make further analyses in the text. The simple analysis of this spectrum (Table 4) and its comparison with that which has been obtained for Mediterranean Africa (Table 2) shows numerous peculiarities:

For a surface at least seven times greater, the number of species is almost three times poorer, whereas the number of genera remains relatively high (615 instead of 916).

The endemic element which represents more than 25% of the flora in Mediterranean Africa here reaches scarcely 12%.

While in Mediterranean Africa there occurs an overwhelming predominance of the Mediterranean element (46% without counting the endemics which would make it closer to 65%), in the Sahara, on the contrary, there is a nearly equal partition between Saharo-Arabian (22.7%), Mediterranean (21.2%) and tropical (32%) elements.

These peculiarities not only confirm the biogeographical heterogeneity of the Sahara but also the hostility of the ecological conditions which now prevail there and which are only reflections of the climatic cataclysms which have occurred there since the end of the Quaternary. Finally, it should be remembered that in the Sahara the major part of the flora is confined in the "massif refugia" or the "zones of safey," while very large surfaces are practically sterile.

## III.2—THE PRINCIPAL BIOGEOGRAPHICAL ELEMENTS

We consider in succession the Saharo-Arabian, Irano-Turanian, Mediterranean, and tropical elements.

III.2.1—*Saharo-Arabian Taxa*

They belong to a large number of the families, but are in fact abundant only in the Boraginaceae (*Lappula, Echiochilon, Moltkia, Arnebia, Gastrocotyle, Megastoma*), the Caryophyllaceae (*Pteranthus, Sclerocephalus, Gymnocarpos, Paronychia, Polycarpaea, Silene*), the Chenopodiaceae (*Schanginia, Sevada*), the Compositae (*Launaea, Atractylis, Gymnarrhena, Lasiopogon, Iphiona, Pulicaria* (including *Frankoeria*), *Anvillea, Asteriscus, Rhetinolepis, Lasiospermum, Chlamydophora*), the Cruciferae (*Reboudia, Farsetia, Savignya, Moricandia, Pseuderucaria, Notoceras, Morettia, Zilla, Schouwia, Anastatica, Robeschia, Torularia, Schimpera, Eremobium*), the Gramineae [*Aristida* (p.p.), *Schismus, Desmostachya, Boissiera*], the Leguminosae (*Trigonella, Lotus, Astragalus, Alhagi*), the Rubiaceae (*Gaillonia*), the Resedaceae (*Reseda*), the Tamaricaceae (*Tamarix*), the Umbelliferae (*Pituranthos, Ammodaucus*) and the Zygophyllaceae (*Zygophyllum, Fagonia, Nitraria*). If a great number of the genera cited above correspond in fact to some elements with Saharo-Mediterranean or Mediterranean-Saharan connections, they nevertheless occupy an appreciable, indeed an important, place in the Saharan flora, and they comprise a large number or reasonably large number of the species with an essentially Saharan or Saharo-Arabian distribution.

III.2.2—*Irano-Turanian Taxa*

Although few, they merit being cited; they appear especially in the eastern Sahara, but some are widespread over most of the Sahara. Let us point out: the Liliaceae (*Bellevalia, Leopoldia*), the Salicaceae (*Populus euphratica* and *Salix subserrata*), the Salsolaceae (*Halocnemum, Salsola, Seidlitzia, Hammada, Noaea*), the Leguminosae (*Astragalus*), the Malvaceae (*Alcea*), the Umbelliferae (*Astoma, Ducrosia, Zosima*), the Boraginaceae (*Paracaryum*), Plantaginaceae (*Plantago*), and the Compositae (*Atractylis, Zoegea, Artemisia*).

III.2.3—*Mediterranean Taxa*

Mediterranean taxa are relatively numerous, as I have noted, and appear (cf. Table 5) among numerous families (especially Caryophyllaceae, Compositae, Cruciferae, Gramineae, Leguminosae, Papaveraceae, Plantaginaceae, Rubiaceae, Scrophulariaceae, Umbelliferae). Their significance is quite variable.

Some appear only in the northern Sahara immediately adjacent to their Mediterranean range and have only a minor biogeographical value. Others are usually located close to areas with water, or are clearly anthropophilous [*Juncus, Scirpus, Polypogon, Ranunculus, Trigonella, Medicago, Trifolium, Frankenia* (p.p.), *Apium, Torilis, Centaurium, Galium, Plantago, Picris, Scorzonera, Lactuca*].

Others, on the other hand, represent isolated colonies, persisting due to relatively favorable ecological conditions, and constituting for the most part vestiges of a flora much more widely spread in the Sahara at the time of the rainy Quaternary periods. The most remarkable case is that from the high Saharan

TABLE 5. The principal biogeographical elements of the families of Saharan Africa. Heading abbreviations are as follows: Gen. = Genera, Sp. = Species, End. = Endemics, S.-A. = Saharo-Arabian, I.-T. = Irano-Turanian, Med. = Mediterranean, Eur. = European, Trop. = Tropical, Oth. = Other.

| Family | Gen. | Sp. | End. | S.-A. | I.-T. | Med. | Eur. | Trop. | Oth. |
|---|---|---|---|---|---|---|---|---|---|
| Acanthaceae | 7 | 10 | . | . | . | . | . | 10 | . |
| Aizoaceae | 11 | 25 | 3 | 1 | . | 1 | . | 20 | . |
| Amaranthaceae | 6 | 14 | . | 1 | 1 | . | . | 7 | 5 |
| Amaryllidaceae | 1 | 5 | . | 3 | . | . | . | 1 | 1 |
| Anacardiaceae | 2 | 5 | . | . | 1 | 2 | . | 2 | . |
| Apocynaceae | 3 | 3 | 1 | . | . | 1 | . | 1 | . |
| Araceae | 2 | 2 | . | . | . | 2 | . | 1 | . |
| Asclepiadaceae | 11 | 23 | 4 | 4 | . | 3 | . | 12 | . |
| Avicenniaceae | 1 | 1 | . | . | . | . | . | 1 | . |
| Balanitaceae | 1 | 1 | . | . | . | . | . | 1 | . |
| Balanophoraceae | 1 | 1 | . | . | . | 1 | . | . | . |
| Boraginaceae | 17 | 43 | 4 | 17 | 2 | 5 | . | 14 | 1 |
| Burseraceae | 1 | 2 | . | . | . | . | . | 2 | . |
| Campanulaceae | 4 | 9 | . | 4 | . | 4 | . | 1 | . |
| Capparaceae | 7 | 23 | . | 1 | . | 1 | . | 21 | . |
| Caryophyllaceae | 22 | 63 | 13 | 13 | . | 26 | . | 7 | 4 |
| Celastraceae | 1 | 1 | . | . | . | . | . | 1 | . |
| Chenopodiaceae | 23 | 64 | 2 | 39 | 6 | 8 | . | . | 9 |
| Cistaceae | 1 | 13 | 4 | 7 | . | 2 | . | . | . |
| Combretaceae | 1 | 1 | . | . | . | . | . | 1 | . |
| Commelinaceae | 3 | 8 | . | . | . | . | . | 8 | . |
| Compositae | 80 | 164 | 13 | 62 | 7 | 44 | . | 32 | 5 |
| Convolvulaceae | 9 | 34 | 2 | 4 | 2 | 2 | . | 20 | 4 |
| Crassulaceae | 2 | 3 | 1 | . | . | 1 | . | 1 | . |
| Cruciferae | 44 | 73 | 12 | 32 | 3 | 23 | . | 2 | 1 |
| Cucurbitaceae | 9 | 14 | . | 1 | . | 1 | . | 12 | . |
| Cupressaceae | 2 | 2 | 1 | . | . | 1 | . | . | . |
| Cyperaceae | 8 | 46 | 2 | 1 | . | 4 | . | 25 | 14 |
| Dipsacaceae | 2 | 6 | 3 | 1 | . | 2 | . | . | . |
| Ebenaceae | 1 | 1 | . | . | . | . | . | 1 | . |
| Elatinaceae | 2 | 5 | 1 | . | . | . | . | 4 | . |
| Ephedraceae | 1 | 8 | 3 | . | . | 5 | . | . | . |
| Ericaceae | 1 | 1 | . | . | . | . | . | . | 1 |
| Euphorbiaceae | 9 | 40 | 5 | 12 | 2 | 5 | . | 16 | . |
| Frankeniaceae | 1 | 6 | 1 | 3 | . | 2 | . | . | . |
| Gentianaceae | 4 | 7 | 2 | . | . | 2 | . | 1 | 2 |
| Geraniaceae | 3 | 15 | 1 | 4 | . | 7 | . | 3 | . |
| Gramineae | 74 | 203 | 19 | 29 | 2 | 50 | . | 76 | 27 |
| Hydrocharitaceae | 5 | 6 | . | . | . | . | . | 4 | 2 |
| Hypericaceae | 1 | 4 | 2 | . | . | 2 | . | . | . |
| Juncaceae | 2 | 10 | . | . | . | 3 | . | . | 7 |
| Labiatae | 16 | 36 | 4 | 5 | . | 18 | . | 7 | 2 |
| Leguminosae | 30 | 153 | 22 | 32 | 7 | 25 | . | 66 | 1 |
| Lemnaceae | 1 | 2 | . | . | . | . | . | . | 2 |
| Lentibulariaceae | 1 | 2 | . | . | . | . | . | 1 | 1 |
| Liliaceae | 11 | 19 | 3 | 4 | 4 | 6 | . | 2 | . |
| Linaceae | 1 | 1 | . | . | . | 1 | . | . | . |
| Loranthaceae | . | . | . | . | . | . | . | . | . |

TABLE 5. *Continued.*

| Family | Gen. | Sp. | End. | S.-A. | I.-T. | Med. | Eur. | Trop. | Oth. |
|---|---|---|---|---|---|---|---|---|---|
| Lythraceae | 3 | 8 | . | . | . | 1 | . | 7 | . |
| Malvaceae | 8 | 32 | 1 | . | 3 | 5 | . | 23 | . |
| Menispermaceae | 2 | 2 | . | . | . | . | . | 2 | . |
| Moraceae | 1 | 6 | 1 | . | . | 1 | . | 4 | . |
| Moringaceae | 1 | 1 | . | . | . | . | . | 1 | . |
| Myrtaceae | 1 | 1 | 1 | . | . | . | . | . | . |
| Najadaceae | 1 | 3 | . | . | . | . | . | . | 3 |
| Neuradaceae | 1 | 1 | . | 1 | . | . | . | . | . |
| Nyctaginaceae | 2 | 9 | 1 | . | . | . | . | 8 | . |
| Nymphaeaceae | 1 | 2 | . | . | . | . | . | 2 | . |
| Oleaceae | 2 | 4 | 1 | . | . | . | . | 3 | . |
| Onagraceae | 3 | 6 | 1 | . | . | 1 | . | 3 | 1 |
| Orchidaceae | 1 | 1 | . | . | . | 1 | . | . | . |
| Orobanchaceae | 2 | 9 | . | 1 | . | 4 | . | 1 | 3 |
| Oxalidaceae | 1 | 2 | . | . | . | . | . | 1 | 1 |
| Palmae | 3 | 3 | . | 1 | . | . | . | 2 | . |
| Papaveraceae | 6 | 15 | 3 | 1 | 4 | 7 | . | . | . |
| Pedaliaceae | 3 | 3 | . | . | . | . | . | 3 | . |
| Plantaginaceae | 1 | 13 | 1 | 2 | 3 | 7 | . | . | . |
| Plumbaginaceae | 3 | 12 | 5 | 5 | . | 1 | . | 1 | . |
| Polygalaceae | 1 | 3 | 1 | . | . | . | . | 2 | . |
| Polygonaceae | 6 | 18 | 3 | 2 | 7 | 4 | . | . | 2 |
| Pontederiaceae | 1 | 1 | . | . | . | . | . | 1 | . |
| Portulacaceae | 1 | 1 | . | . | . | . | . | . | 1 |
| Potamogetonaceae | 1 | 10 | 1 | . | . | . | . | 1 | 8 |
| Primulaceae | 3 | 3 | 1 | . | . | . | . | . | 2 |
| Ranunculaceae | 5 | 11 | 1 | . | 6 | 2 | . | . | 2 |
| Resedaceae | 5 | 13 | 2 | 7 | . | 2 | . | 2 | . |
| Rhamnaceae | 4 | 6 | . | 1 | 1 | 3 | . | 1 | . |
| Rhizophoraceae | 1 | 1 | . | . | . | . | . | 1 | . |
| Rosaceae | 3 | 4 | 1 | . | 2 | . | . | . | . |
| Rubiaceae | 9 | 22 | 4 | 1 | 1 | 8 | . | 8 | 1 |
| Ruppiaceae | 1 | 1 | . | . | . | . | . | . | 1 |
| Rutaceae | 1 | 1 | . | 1 | . | . | . | . | . |
| Salicaceae | 2 | 2 | . | . | 2 | . | . | . | . |
| Salvadoraceae | 1 | 1 | . | . | . | . | . | 1 | . |
| Santalaceae | 2 | 2 | . | . | . | 2 | . | . | . |
| Sapindaceae | 2 | 2 | . | . | . | . | . | 2 | . |
| Sapotaceae | 1 | 1 | . | . | . | 1 | . | . | . |
| Scrophulariaceae | 16 | 49 | 7 | 8 | 1 | 14 | . | 15 | 4 |
| Selaginaceae | 1 | 1 | . | 1 | . | . | . | . | . |
| Simaroubaceae | . | . | . | . | . | . | . | . | . |
| Solanaceae | 6 | 21 | 1 | 3 | . | 3 | . | 8 | 6 |
| Sterculiaceae | 4 | 6 | . | . | . | . | . | 6 | . |
| Tamaricaceae | 2 | 15 | 1 | 11 | 2 | 1 | . | . | . |
| Thymelaeaceae | 1 | 1 | . | . | . | 1 | . | . | . |
| Tiliaceae | 3 | 9 | . | . | . | . | . | 9 | . |
| Typhaceae | 1 | 2 | . | . | . | . | . | 2 | . |
| Umbelliferae | 18 | 35 | 13 | 5 | 3 | 12 | . | 2 | . |
| Urticaceae | 3 | 6 | . | 3 | 1 | . | 2 | . | . |
| Vahliaceae | 1 | 2 | . | . | . | . | . | 2 | . |

TABLE 5. *Continued.*

| Family | Gen. | Sp. | End. | S.-A. | I.-T. | Med. | Eur. | Trop. | Oth. |
|---|---|---|---|---|---|---|---|---|---|
| Valerianaceae | 1 | 2 | . | . | . | 2 | . | . | . |
| Verbenaceae | 6 | 7 | 1 | . | . | 1 | . | 5 | . |
| Vitaceae | 2 | 2 | . | . | . | . | . | 2 | . |
| Zannichelliaceae | 2 | 5 | . | . | . | . | . | 3 | 2 |
| Zygophyllaceae | 8 | 43 | 10 | 25 | 2 | . | . | 6 | . |
| TOTALS | 617 | 1,620 | 190 | 359 | 75 | 344 | 2 | 524 | 126 |
| PERCENTAGES | | | 11.6 | 22.2 | 4.5 | 21.2 | 1.2 | 32.3 | 7.7 |

mountains (Quézel, 1965:220) where persist about 27 species common to Hoggar and Tibesti, 26 belonging to the central Saharan Massif, and 7 or 8 limited to Tibesti, beside some 25 species with a Saharo-Mediterranean connection, and a certain number of endemics of Mediterranean origin (cf. below).

Without repeating here this complete list, some especially remarkable species may be noted: *Ephedra major, Luzula atlantica, Carex distans, Osyris alba, Anethum graveolens, Clematis flammula, Pistacia atlantica, Rhus tripartitum, Nerium oleander,* and *Celsia longirostris.*

Another refugium for the Mediterranean elements is formed by the Atlantic coast where appear: *Asparagus altissimus, Osyris alba, Frankenia pulverulenta, F. corymbosa, Convolvulus fatmensis, Lycium intricatum, Rhus oxyacantha, Launaea arborescens, Periploca laevigata,* and *Phagnalon purpurascens.*

III.2.4—*Tropical Taxa*

These constitute, percentage-wise, the most prevalent element in the Sahara, which is not without interest for biogeographical interpretation. As I stated earlier, the southern portion of this desert is heavily populated by essentially tropical elements. Elsewhere, besides a basic group with a tropical background, which is present almost everywhere except in the northen Sahara, and which forms part of the landscape of "Savanes désertiques à Acacia-Panicum" (Maire, 1940), the tropical element appears also in the Sahara in certain preferential points and in particular on the southern slope of the Saharan mountains, but also on their Piedmont, where, as at Tibesti (Quézel, 1958), it can form a true enclave of Sahelian vegetation. The coastal links of the Red Sea in Egypt, as well as the valley and the delta of the Nile, also offer a rich procession of tropical species in a zone with a Saharan climate. All these factors explain the important development of the tropical element (sensu lato) in the Sahara. It is appropriate to consider different assemblages in succession.

III.2.4.1—*Sahelian Taxa* (Fig. 6).—Sahelian taxa are certainly the most numerous. They are divided into many families, of which some hygrophiles (Avicenniaceae, Balanophoracae, Elatinaceae, Hydrocharitaceae, Rhizophoraceae) are especially common in Egypt. The landscape of desert savanna, and the Sahelian enclaves of the Saharan mountains are in principle richer in Sahelian elements as one progresses towards the south (under similar climatic conditions).

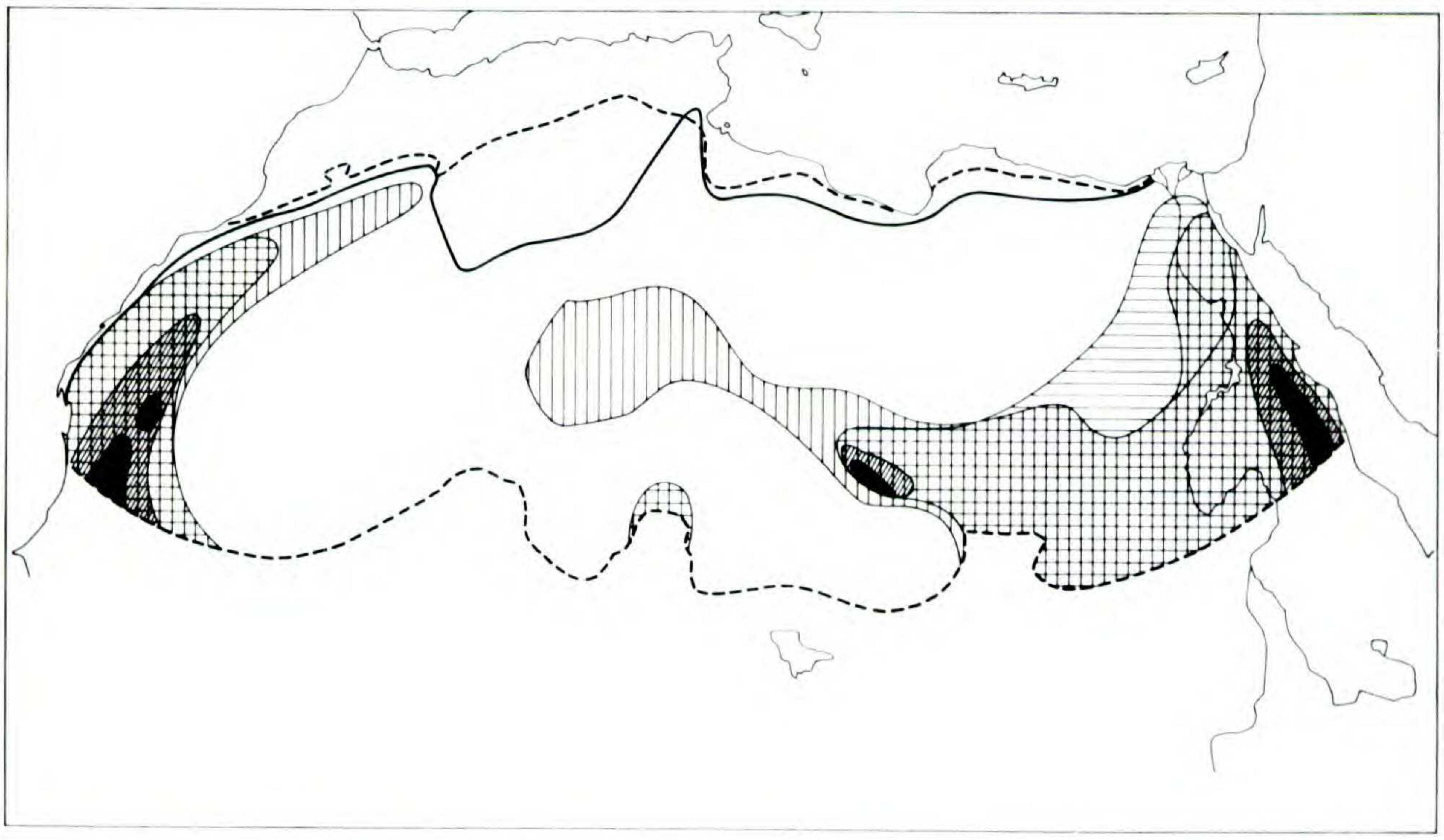

FIGURE 6. Distribution of Sahelian elements in Saharan Africa.—Heavy black line indicates the northern limit of *Acacia raddiana*.—Vertical lines indicate the area of distribution of *Balanites aegyptiaca* and *Moerua crassifolia*.—Horizontal lines indicate the area of *Capparis decidua*.—Diagonal lines indicate the area of the genus *Cadaba*.—Solid black indicates the area of *Boscia senegalensis*.

It is for this reason that the *Acacia raddiana* and *Ziziphus lotus* association of the northwestern Sahara possesses only 2.4% tropical elements while north of Hoggar, the *Panicum turgidum* and *Cassia aschreg* association reaches 12.6%, and further south, the *Cassia lanceolata* and *Tephrosia leptostachya* association reaches 39.9% (Quézel, 1965).

The valley and the delta of the Nile certainly represent a zone highly favorable to the development of the Sahelian taxa, as much as a result of local ecological conditions as a result of the permanent contribution of diaspores of African origin by the river, more particularly before the construction of the Aswan Dam.

From the floristic point of view and without entering into detail, the following families are best represented: Gramineae (with 40 genera and in particular, *Saccharum, Brachiaria, Cenchrus, Tragus, Latipes, Dinebra, Digitaria, Aristida, Sporobolus, Enneapogon, Eragrostis*), Leguminosae (*Crotalaria, Indigofera, Tephrosia, Sesbania, Taverniera, Rhynchosia, Cassia, Acacia*), Compositae (*Blumea, Conyza, Geigeria, Eclipta*), but also Aizoaceae (*Mollugo, Giesekia, Trianthema*), Capparaceae (*Capparis, Boscia, Cadaba, Maerua, Cleome, Crataeva*), Moringaceae, Vahliaceae, Burseraceae, Sapindaceae, Salvadoraceae, Tiliaceae (*Grewia, Corchorus*), Malvaceae (*Abutilon, Hibiscus, Sida*), Sterculiaceae, Combretaceae, Asclepiadaceae (*Calotropis, Glossonema, Oxystelma, Leptadenia, Pentatropis*), Boraginaceae (*Cordia, Trichodesma*), Verbenaceae, Scrophulariaceae (*Anticharis, Lindbergia, Sutera, Bacopa, Peplidium*), Acanthaceae (*Blepharis, Bar-*

*leria, Peristrophe, Justicia, Ruellia, Monechma*), and Pedaliaceae (*Sesamum, Pedalium, Rogeria*).

III.2.4.2—*African Highland Taxa.*—Highland taxa are abundantly prevalent in Tibesti, where besides endemic species which also belong there, it is appropriate to note miscellaneous ferns, specifically *Asplenium aethiopicum, Hypodematium crenatum*, but also *Acacia seyal, A. laeta, Ochradenus baccatus, Erhetia obtusifolia*, several *Ficus* species, *Hermannia abyssinica, Malhania ovata, Conyza abyssinica, Vernonia amygdalina*, as well as several species of *Abutilon* and *Convolvulus*. One must add to them *Satureia biflora, Silene kiliani*, present as well at Hoggar.

III.2.4.3—*Tropical Elements on Mountain Massifs Next to Coasts.*—The floristic inventory of the massifs adjoining the Atlantic, especially those which in Egypt border the Red Sea, demonstrates the appearance of a contingency important for tropical species, namely, the substitution of an increase in the rate of the atmospheric humidity, for infrequent, indeed almost total absence, of precipitation.

It is for this reason that numerous tropical genera appear on Zemmour, especially on the Adrar of Mauritania, which in general are present in the Sahara in the south (*Barleria, Blepharis, Peristrophe, Cleome, Combretum, Pluchea, Momordica, Bergia, Crotalaria, Indigofera, Tephrosia, Melhania, Bouchea*), but also *Tamarindus indica, Bauhinia rufescens, Jatropha*. However, this phenomenon remains quite limited.

In contrast on the shore of the Red Sea, and in particular towards the Sudanian frontiers, numerous tropical elements occur, which, besides some common types, include numerous elements belonging in general to some East African elements. Some 30 genera occur here which belong to this category. The most remarkable are, without a doubt, *Onychium, Sphaerocoma, Cometes, Puppalia, Psilotrichum, Taverniera, Delonix, Dodonea, Waltheria, Euclea, Enicostema, Jaubertia, Osteospermum, Aneilema*, and certainly not forgetting *Dracaena ombet*. Although this region is still situated in the Saharan climatic zone, it is difficult to integrate it into the Saharan phytogeographic domain.

III.2.4.4—*Elements of the tropical eremic flora or "Rand Flora."*—The existence of a xerophylic flora, indeed eremic of tropical origin, was, it seems, noted for the first time by Christ. It is Lebrum (1947) who named this group "Rand Flora," a term used again by Monod (1957) and by numerous others.

In spite of the implied unanimous accord presently existing on this question, the difficulty appears in fixing the exact boundaries of this flora which, theoretically, is found in the arid zones of tropical Africa both north and south. Many taxonomic uncertainties remain. It appears, however, possible to attribute to it several elements still present in the Canaries, such as cactoid *Euphorbia*, the genera *Caralluma* and *Dracaena*, and doubtlessly quite a large number of genera and species now present in the Sahara, such as: *Aristida* (p.p.), *Asthenatherum, Oropetium* (Fig. 7), *Enneapogon, Orygia, Cocculus, Neurada, Colocynthis, Monsonia, Ifloga, Caylusea, Oligomeris*, etc.

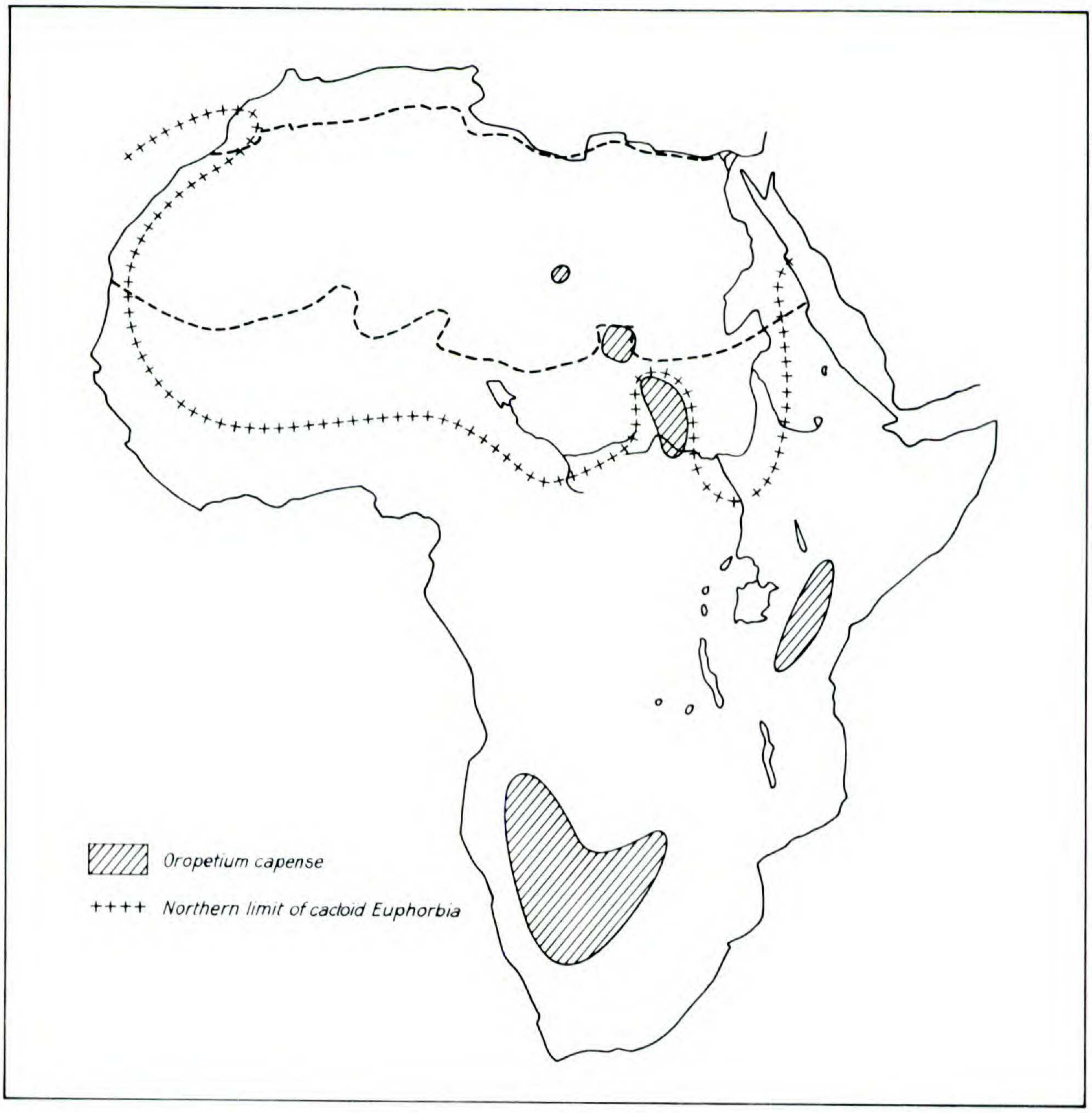


FIGURE 7. Distribution of several members of the tropical eremic flora or "Rand Flora."

### III.2.5—*Pluro-Regional Elements*

In conclusion should be mentioned the existence in the Sahara of taxa with areas of distribution overlapping different biogeographical subdivisions and stretching in particular from tropical Africa, indeed southern Africa, to the Mediterranean region and finally perhaps quite close to the "Rand Flora." The case of the Gramineae, especially the Andropogoneae, alluded to earlier, can again be noted since these species are almost all present in the Sahara and in particular on the Saharan mountains. But it is advisable to cite several others (apart from hygrophilous or anthropophilous species without great significance), particularly *Commicarpus plumbagineus* and *Maytenus senegalensis*.

The same is true for *Erica arborea*, whose discovery in the Tibesti Massif (Bruneau de Miré & Quézel, 1959) was one of the greatest surprises furnished by the botanical exploration of this massif (Fig. 8).

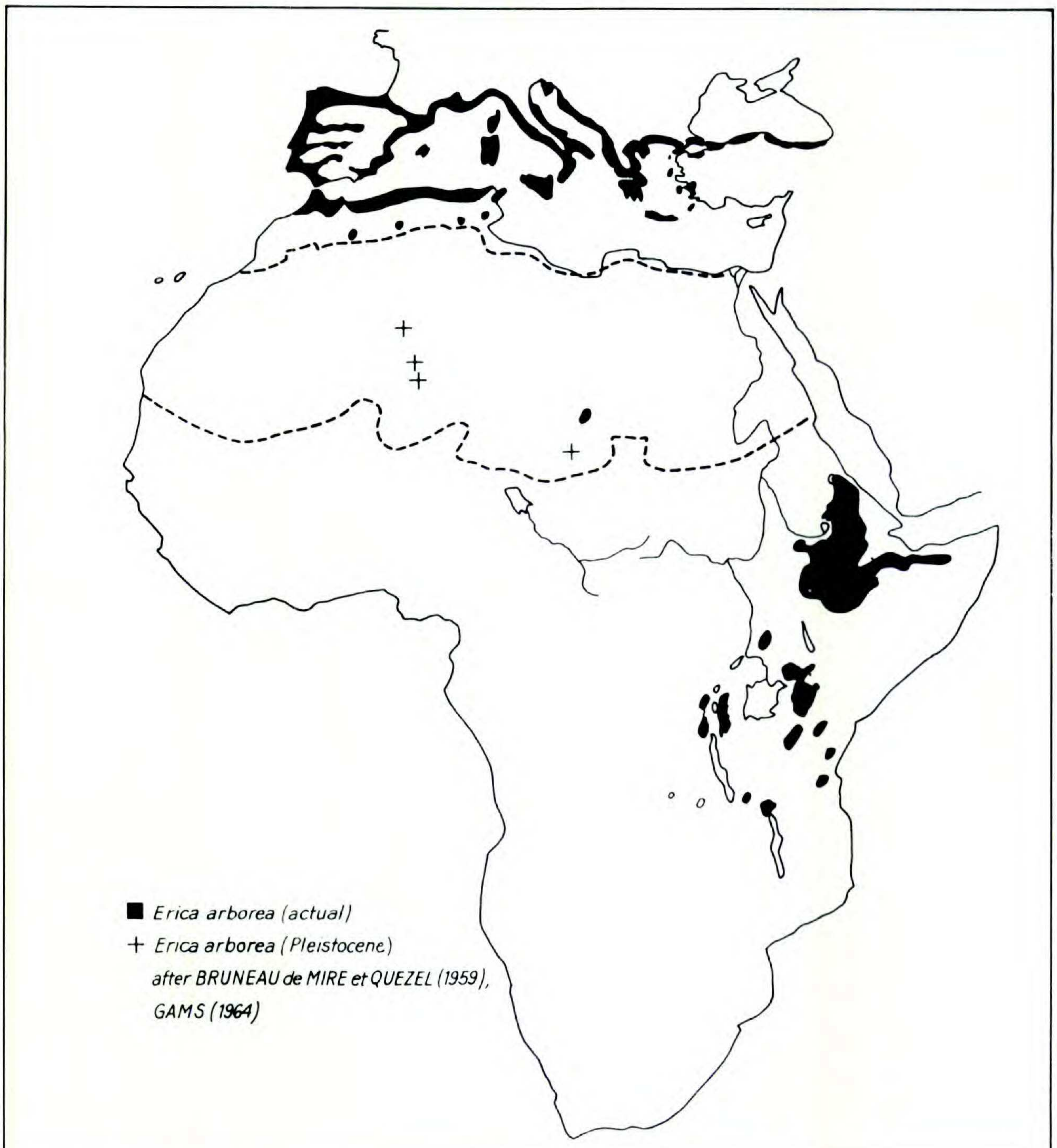


FIGURE 8. Distribution of *Erica arborea*; solid black indicates the present distribution, crosses indicate Pleistocene sites; after Bruneau de Miré & Quézel (1959), Gams (1964), and Straka (1970).

## III.3—ENDEMISM IN THE SAHARA

### III.3.1—*Generic Endemism*

Generic endemism in the Sahara (Quézel, 1964a) is clearly less developed than in Mediterranean Africa; only 16 genera can in fact be cited here, and some of them overlap more or less extensively into the Mediterranean region. It is remarkable to consider that for the entire subregion of the Sahara, it is the northwestern zone of the Sahara which is by far the richest in endemic genera

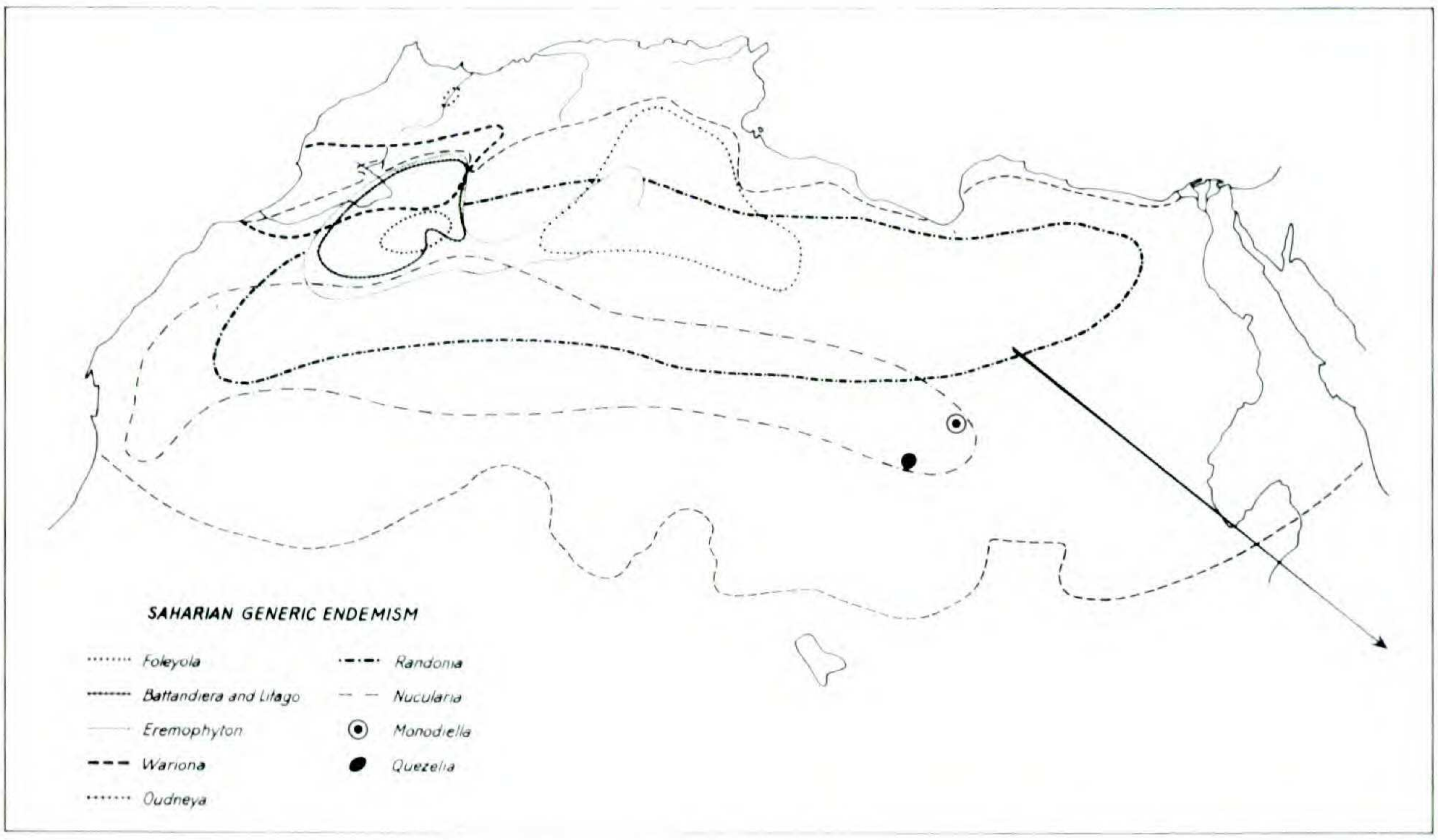


FIGURE 9. Distribution of endemic genera in the Sahara.

(Fig. 9). Indeed, *Battandiera*, *Lifago* and *Foleyola* are localized there and three others overlap more or less abundantly in this sector: *Eremophyton*, *Warionia*, and *Stephanochilus*.

The genera *Oudneya* and *Ammosperma* are south-Algerian-Moroccan in the major part of their distribution with one species, *O. zygarrhena*, in the Saharan enclave of the Moulouya valley.

*Perralderia*, *Tourneuxia*, *Rhanterium*, *Megastoma*, and *Nucularia* occupy much larger areas, but do not seem to spread into Libya towards the east. *Randonia*, on the other hand, reaches Egypt and Somaliland.

Finally, it is appropriate to note the rarest genera from Tibesti: *Mondiella* and *Quezelia*; the genus *Tibestina* has, however, been synonymized (Scholtz, 1974)

Indeed, of the 16 genera, some (*Stephanochilus*, *Lifago*) are even considered by some authors as mere sections (of the genera *Centaurea* and *Filago*). It is a question then of 6 Compositae, 5 Cruciferae, and only 1 representative of the Liliaceae, Chenopodiaceae, Boraginaceae, Gentianaceae, and Resedaceae.

Still of 16 genera, 14 are monospecific: *Battandiera*, *Lifago*, *Foleyola*, *Eremophyton*, *Warionia*, *Perralderia*, *Tourneuxia*, *Randonia*, *Rhanterium*, *Megastoma*, *Nucularia*, *Monodiella*, *Quezelia*, and *Stephanochilus*. The two others are bispecific.

All these genera are very diversified from the taxonomic viewpoint, and must certainly be associated with the paleoendemic element. The very small area occupied by some of them and the almost exclusive preponderance of monospecific types permit one to consider most of them as residual elements. Furthermore *Warionia* constitutes the only representative of the tribe Mutisiae.

III.3.2—*Specific Endemism*

Here again the remarkable fact is the very striking reduction of numbers of species in the heart of the Saharan flora. In spite of inherent difficulties with this question, we have cataloged 189 endemic species for the entire Saharan flora (Arabia excluded). This represents 11.9% of the entire flora as opposed to 25% in Mediterranean Africa.

The percentage of genera with endemic species is also lower in the Sahara (116 of 615 for 19%) than in Mediterranean Africa (330 of 925 for 37%).

It is also interesting to note the total disappearance in the Sahara of genera with high endemic rates; here only 8 genera have more than 4 endemic species. The generic representation of the endemism is the following: 6 endemic species: *Astragalus* and *Fagonia*; 4 endemic species: *Euphorbia*, *Ferula*, *Helianthemum*, *Phagnalon*, and *Zygophyllum*; 3 endemic species: *Bromus*, *Calligonum*, *Lotus* and *Silene*. Finally, 25 genera possess 2 endemic species and 78 a single one.

III.3.3—*Biogeographical Significance of Endemic Taxa*

Among the some 200 species which can be considered endemic in the territory of the Sahara a great number pose interesting problems, especially historical problems. Some will be examined later on.

III.3.3.1—*Endemics of Mesogean Origin.*—These endemics are indisputably the most numerous (about 90). They correspond both to endemics of Mediterranean origin and to those of Saharo-Arabian origin. It is necessary to note that it is often difficult to establish a precise limit between these two groups, and certain genera, indisputably of Mediterranean origin, have evolved some endemic species in the Sahara whose distribution is of the Saharan type. I will consider them, nevertheless, as endemics of Mediterranean origin.

*Endemics of Mediterranean Origin.*—Their list is long and I will discuss them as a function of their geographical distribution.

Some are found for the most part in the Sahara: *Koeleria rohlfsii*, *Diplotaxis acris*, *Lotus jolyi*, *L. roudairei*, *Astragalus akkensis*, *Euphorbia calyptrata*, *Megastoma pusillum*, *Antirrhinum ramosissimum*, *Atractylis aristata*, and *Volutaria leucantha*.

The northern Sahara to the south of the Maghreb offers: *Urginea noctiflora*, *Astragalus gombo*, *A. gombiformis*, *Genista saharae*, *Daucus biseriatus*, *Helianthemum eriocephalum*, *H. getulum*, *Euphorbia guyoniana*, *Convolvulus supinus*, *Anthemis sabulicola*, *Chrysanthemum macrocarpum*, *Pulicaria laciniata*, *Centaurea furfuracea*, *Stephanochilus omphalodes*, *Atractylis delicatula*, *A. carduus*, and *Heliotropium digynum*. The following species are, on the other hand, much more localized: *Atriplex mollis*, *Scabiosa camelorum*, *Astragalus kralikianus*, *Volutaria saharae*, and *Rupicapnos muricaria*.

The western Sahara has in its area: *Diplotaxis pitardiana*, *Moricandia foleyi*, *Convolvulus trabutianus*, *Withania adpressa*, *Ormenis eriolepis*, *O. lonadioides*, and *Atractylis babelii*.

In oceanic Sahara can be noted: *Lotus chalazei*, *Anethum foeniculoides*, *A.*

*theurkhaufii, Ephedra rollandii, Teucrium chardinianum,* and several species of *Limonium.*

In the eastern Sahara occur: *Dianthus guessfeldtianus, D. sinaicus, Biscutella elbensis, Meliotus serratifolia, Onosma galalense,* and *Pterocephalus aramicus.*

Some species belonging to the element with Saharo-Mediterranean connections can also be noted here; they are especially frequent in the northern half of the Sahara: *Reboudia erucarioides, Pseuderucaria teretifolia, Alyssum macrocalyx, Matthiola maroccana, Echium trigorrhizum, Marrubium desertii, Plantago akkensis, Senecio massaicus, Peralderia coronopifolia, Rhantherium suaveolens,* and several species of *Ferula.*

It is appropriate again to list under a special heading the remarkable endemics localized in the Saharan mountains.

Here may be noted *Olea laperrini, Cupressus duprezziana,* and *Myrtus nivellei* (Fig. 10). In fact, as we already indicated (Bruneau de Miré & Quézel, 1961), it is probable that the Saharan Olivier is linked with African sources. I will discuss this problem later. Belonging on this list from Hoggar and its extensions and from Tibesti are: *Verbascum dentifolium*; from Teffedest: *Astragalus geniorum, Helianthemum geniorum*; and from Tibesti: *Stipa tibestica, Celsia tibestica, Eragrostis kohorica, Foeniculum scoparium, Erodium oreophilum* and *Spergularia tibestica,* a local variant of *S. fontenellei* of Hoggar, where *Phagnalon garamantum* also appears.

Some other endemics localized in the mountainous areas are more likely associated with eastern Mediterranean sources: *Vartemia sericea* to *V. iphionoides, Campanula bordesiana* and *C. monodiana* with several Mideastern species.

Finally, although not endemics, several species with disjunct distributions merit being noted in this group. This is the case for *Erodium meynieri* and *Hypericum psilophytum* (south Morocco and the central Saharan Massif), *Centaurea touggourensis* (Hoggar and Bellezma), *Conyza triloba* (*Erigeron trilobus*) and *Senecio hoggariensis* (southern border of Maghreb, Hoggar, Tibesti, Sinai).

*Endemics of Saharo-Arabian Origin.*—They are clearly less numerous. Some genera, however, have evolved a certain number of taxa. The most remarkable belong to the Zygophyllaceae (Ozenda & Quézel, 1956), particularly *Fagonia* where, in spite of great difficulties of taxonomic rank, it seems possible to discern at least 6 endemic species, of which 3 are in the eastern Sahara; the genus *Zygophyllum* encompasses 4 endemic species, of which 2 are in oceanic Sahara (*Z. gaetulum* and *Z. waterlotii*). The genus *Calligonum* also has 3 endemic species of which 1, *C. azel,* with a wide distribution and the 2 others, *C. calvescens* and *C. arich,* are located between southern Tunisia and Tassili. Also included here is the genus *Limoniastrum* including, besides 1 Saharo-Mediterranean species (*L. guyonianum*), species occurring especially in the southern Morroco and in part of the Mediterranean regions (*L. feei, L. ifniensis, L. weygandiorum*). In the western Sahara the genus *Echiochilon* evolved *E. chazaliei* and *E. simmoneaui.* Finally, in the northern Sahara, we can note *Enarthrocarpus clavatus, Eremophyton chevalieri, Moricandia foleyi* among the crucifers and *Pituranthos battandieri* and *P. triradiatus* among the Umbelliferae. In the Chenopodiaceae

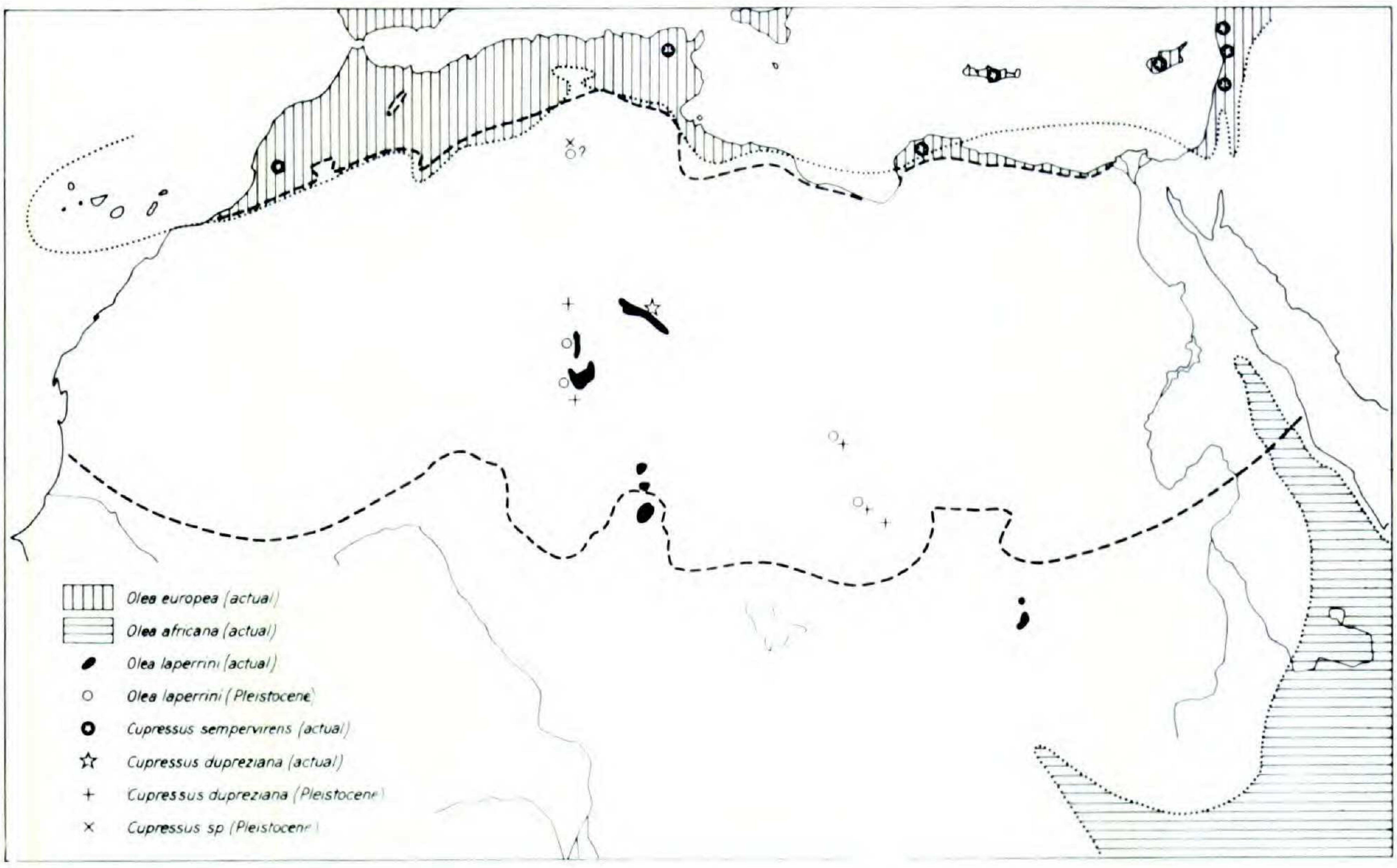


FIGURE 10. Distribution of Saharan mountain endemics compared with those of related species and known Pleistocene sites.

the genus *Anabasis* is represented by *A. aretioides* and *A. oropediorum* of the southern flank of the Saharan Atlas and *Suaeda* by *S. monodiana*, *S. ifniensis*, and *S. arguinensis* of oceanic Sahara. Also added can be *Pulicaria volkoskyana* of the southern Sahara and *Salvia chudeaui*, a vicariant of *S. santolinifolia* of the Sind, *Anvillea radiata*, *Gaillonia reboudiana*, and several representatives of the genus *Tamarix*, always a difficult group to interpret.

III.3.3.2—*Endemics of European Origin.*—Listed, because of lack of a better way, besides endemics of Mesogean origin, are some species whose affinities are debatable but whose affinities derive more from European and Eurasian taxa. The majority of them are localized on the summit of Tibesti where *Ephedra tilhoana*, *Artemisia tilhoana*, *Asplenium quezellii*, *Hyoscyamus tibesticus*, and *Galium uniflorum* appear as relatives of *E. distachya*, *A. alba*, *A. lepidum*, *H. albus*, and *G. spurium*. The case of *Helosciadium muratianum* and *Epilobium mirei* from the lakes of Borkou is comparable as these species are very close to *H. nodiflorum* and *E. parviflorum*. Finally *Erythrea minutissima* from Aozou in Tibesti, doubtlessly derives from *E. pulchella*, and in Hoggar *Potamogeton hoggariensis* from *P. pusillus*.

III.3.3.3—*Endemics of Tropical Origin.*—The endemics of tropical origin are less numerous in the Sahara than the endemics of Mediterranean origin despite the numerical dominance of the tropical element. In fact, with very rare exceptions the endemics of tropical origin occur only in special territories, especially in the mountains of the Sahara and coastal zones; the southern Saharan fringe likewise represents a very special case. As a result, the Sahara does not feature endemics of tropical origin for 9/10 of its surface, with the exception, however, of *Crotalaria saharae*, and perhaps also *Lotononis dichotoma*. It is evident that this peculiarity traces to a recent, indeed extremely recent, origin from a floristic background of the Sahelian type in the Sahara.

I shall examine successively the endemics more or less associated with the Sahelian flora, those which belong to the "Rand Flora," and finally tropical endemism of the montane type.

*Endemism of Sahelian Origin.*—It is manifested fundamentally in the southern Sahara, even on the southern bases of the Hoggar and Tibesti massifs. Certain species are, from all evidence, recently evolved micromorphs, such as *Pegolettia dubieffiana* and *Bergia mairei* (Quézel, 1954) on the southern base of Hoggar derived from *P. senegalensis* and from *B. suffruticosa*. In the northern Sahara *Sporobolus tourneuxii* (southern Tunisia) and *S. lanuginellus* (southern Morocco) belong without a doubt to this group, as well as the rare *Crotalaria vialattei*.

On the other hand, although one often lacks scientific contributions to the exact division of these species, there truly seems to exist, on the mountain massifs of the southern Sahara, quite a collection of species which appear to be primarily limited to this zone, even if they penetrate locally in the Sahelian territory (notably on the northern mountain massifs Adrar of Mauritania, Air and Ennedi). Such appears to be the case for *Coelachyrum oligobrachiatum* and *C. brevifolium*, *Cenchrus montanus*, *Eleusine flagellifera*, several *Tribulus* (*T. alatus* and *T. ochroleuchus*), *Anticharis linearis*, *Blumea gariepina*, and on the Adrar of Mauritania for *Barleria schmittii*.

*Endemism at the Level of the "Rand Flora."*—A certain number of endemic species appear to be able to be referred to this source, which we have characterized precisely above. Such is the case for the endemics belonging to the genera *Caralluma* (*C. venenosum*, *C. sinaica*), *Mesembryanthemum* (*M. theurkhaufii*, *M. gausseni*), *Wahlenbergia* (*W. etbaica*, *W. tibestica*, *W. bernardi*), and also *Lotononis riouxii*.

It is likely that the elements generally considered to be of Macaronesian origin ought to be included here. This is the case for the cactoid euphorboids, and in particular for *Euphorbia balsamifera* and *E. regis-jubae*, as well as a certain number of species designated above as belonging to the Mediterranean flora (*Kalanchoe faustii*, *Commelina rupicola*) which extend more or less into the Saharan zone.

*Endemism of the Montane Type.*—I have already analyzed this on several occasions (Quézel, 1958, 1964a) and will here only recall the conclusions.

*Montane Endemics of Indigenous Origin.*—In this category is united a small group of species which represent vestiges of an indigenous predesert flora of the massifs. Such is the case for: *Pentzia monodiana*, *Ficus teloukat*, *Commicarpus montanus*, *Bidens minuta*, *Pluchea crenata*, *Tripogon multiforum*, as well as a group of vicariant endemics belonging to the genus *Rhynchosia* (*R. lynesii*, *R. tibestica* and *R. airica*).

*Endemics of African Highland Origin.*—These are taxa derived from lines still largely found on the tropical African mountains and the Ethiopian plateaus.

We can cite *Albuca septentrionalis, Chloris tibestica, Clematis tibestica, Trichodesma giganteum, Pentas tibestica,* and *Phagnalon tibesticum,* vicariants, respectively, and truly extremely closely related to *A. abyssinica, C. notocoma, C. simensis, P. carnea,* and *P. hypoleucum.*

*Endemics of Montane-African Origin.*—All localized on the summit of Tibesti, despite their rarity, they represent one of the most remarkable curiosities of the massif in a singular ecological environment, where *Erica arborea* also appears. The following can be cited: *Agrostis tibestica, Avenastrum tibesticum, Festuca tibestica, Silene mirei, Crassula tibestica, Helichrysum monodianum, Dichrocephala tibestica,* respectively related to *A. pilgeriana, A. lachnantha, F. abyssinica, S. macrosolen, C. pentandra, H. foetidum,* and *D. chrysanthemifolia* (Bruneau de Miré & Quézel, 1959). *Nepeta tibestica* is near several Ethiopian species.

Finally, on Tibesti exist rare endemics of Sudanese origin, localized particularly at the level of the fumaroles of Touside, at approximately 3,000 m altitude: *Oldenlandia toussidana* close to *O. goreensis* and *Fimbrystilis minutissima* vicariant of *F. oligostachys.*

## IV.—Historical Interpretation of the Vegetative Population of Mediterranean and Saharan Africa

The present flora of Africa now situated to the north of the Sudano-Angolan floristic region is considered to be the result of paleoclimatological, paleoecological, and paleogeographical influences, persisting since approximately the beginning of the Tertiary, on the different vegetative assemblages which have evolved there but also on those which have been able to migrate there for various reasons.

The interpretation of these phenomena is extremely complex, and it would be ill-timed to try to give an analysis of it here, besides all is relative and subject to caution. However, a certain number of scientific papers, in general recent, have brought to these questions new precise details and actually permit one to comprehend, if not the totality of the phenomena, at least part of them.

These contributions have essentially treated the paleoclimatological and paleobotanical aspects.

### IV.1—Contributions of Paleoclimatology and Paleobotany

We begin with a consideration of the Paleocene.

#### IV.1.1—*Paleocene*

If one looks at it somewhat diagrammatically and if one confines it essentially to the African continent, it seems likely that the regions studied here were affected in the Paleocene by a climate essentially of the equatorial type over the entire current Sahara (Millot, 1964; Greenway, 1970) and assigned by the latter to a "Tropical Rain Forest." The true Maghreb was related to a cooler climate, permitting the formation of a "Temperate Rain Forest." But Africa, a part of Gondwanaland, has not been reunited to Eurasia, as according to Dewey et al.

(1973) the connections between these two continents would not be prior to the middle Miocene.

From the point of view of the vegetation it appears that the Paleocene flora has not played an important role in the formation of the true Mediterranean Saharan stock, as is confirmed by the findings of Boureau (1958), and in palynology by those of Roche (1974), Jardine et al. (1974). Inversely, it is to this period that a large portion of the biogeographical affinities existing between the ancient and the new continent are affirmed, since America and Europe remained in contact at least to the middle Cretaceous.

If the flora corresponding to this period is well known in the Sahara, the same is not true for the region corresponding to the present Maghreb. The results obtained by Medus (1971) for the Mesogean Cretaceous flora remain in effect without significance for the later flora, the plant groups represented by *Classopolis* and *Normapolles* appearing to be end points.

On the other hand, it is very probable that the establishment of the very numerous taxa common between Europe and North America dates from this period in an area north of the Tethys (Raven, 1973).

The same is true for the meso-hygrophylic flora (*Acer*, *Aesculus*, *Cercis*, *Carpinus*, *Epimedium* incl. *Vancouveria*, *Fraxinus*, *Euonymus*, *Ostrya*, *Platanus*, *Populus*, *Quercus*, and also *Pinus* and *Juniperus* etc.) and the meso-xerophytic flora (*Arctostaphylos*, *Amelanchier*, *Arbutus*, *Berberis*, *Celtis*, *Helianthemum*, *Lavatera*, *Lycium*, *Rhamnus*, *Rhus*, *Salvia*, *Styrax*, *Smilax*, *Viburnum*) or also the xero-eremic flora (*Aristida*, *Boerhavia*, *Fagonia*, *Frankenia*, *Cleome*, *Evax*, *Talinum*, *Trianthema*, etc.).

The existence of a more or less xeric flora in Africa appears probable in this period, in particular in the southeastern part of southern Africa where Greenway identified a "subtropic woodland shrub" where, at least in part, the ancestors of the "Rand Flora" could have evolved. In contrast, because of the position of the equator, nothing like it appears to have existed in North Africa.

IV.1.2—*Oligo-Miocene*

The displacement of the equator toward the south permitted the formation in Africa of climates and types of vegetation closer to those presently observed, especially in the southern portion (Axelrod & Raven, 1978).

In the Oligo-Miocene present north tropical Africa was essentially occupied by a "temperate rain forest" in the area of the present Sahara, and by a "subtropical woodland savana" in the area of the present Mediterranean region, with a sclerophyllous "subtropical evergreen forest" on the mountains. According to Axelrod and Raven, this woodland savanna, by its floristic composition (Caesalpinieae, Mimoseae, Pittosporaceae, Combretaceae) seemed already characteristic of a climate with the presence of a dry period.

The sclerophyllous forest of North Africa with a dominance of *Quercus*, *Juniperus*, *Pinus*, *Laurus*, *Pistacia*, and *Olea* seems to have evolved in the Miocene and to have extended itself into the Pliocene.

Several important phenomena deserve emphasis in this period: in tropical

Africa there is the evolution of a montane flora in the region of the volcanic massifs which, incidentally, have allowed some notable floristic and faunistic exchanges (Hedberg, 1965) between northen Africa and the tropical south since the Miocene. Similarly, the appearance of considerable relief should have multiplied biotypes favorable to the expansion of a xerophytic flora (especially the "Rand Flora") of tropical origin.

Finally, more to the north, the existence of arid phases in what is presently the Maghreb, associated with the building of mountain chains elevated on the site of the Tethys, constituted a millieu eminently favorable to the speciation and migration, especially from the east to west, of the floras (Stebbins, 1974).

IV.1.3—*Pliocene*

If the existence of phases of aridity and in particular the appearance of at least a local or temporary dry season was already recognizable in the Miocene in northern Africa, it was in the Pliocene that this worsening of the climate was accentuated. The appearance of the first eolian deposits in the Sahara (Butzer & Hansen, 1968), date from the beginning of the Pliocene, and Coppens & Koeniguer (1976) indicate that in the Koro-Toro region *Tamarix* and *Retam* forests were part of a prehistoric stratum dated 4–5 million years. Maley (1977) provides several paleontological and geomorphological arguments for this interpretation and thinks that it is in this period that the desert climate started to establish itself in northern Africa, paralleling a perceptible lowering of the temperature in the Mediterranean region (de Lumley, 1976).

The palynological analyses carried out at Hoggar by Van Campo et al. (1965), and then at Kourkour in Egypt (Van Campo et al., 1968) on sediments dating from the end of the Pliocene, demonstrate, without entering into the fine points of the discussion, a flora ultimately rather closely resembling the present flora, and one in which elements called Saharan and tropical predominate; the presence of pollen belonging to northern taxa appears more related to long distance transport. In Saoura (Van Campo, 1973) the results were comparable for the most part.

It seems, therefore, that from the Pliocene, and with an influence more or less great throughout this period, a desert climate established itself in the major part of the Sahara, at least in the lower altitudinal zones. Thus desertification began at least 5–6 million years ago and certainly increased up to the first pluvial phases of the Pleistocene, in direct correlation with the advent of the glaciations.

In Mediterranean Africa, on the contrary, paleobotanical contributions demonstrate a very diversified flora in the Villafranchian in which occurred, besides tropical elements or Macaronesian elements presently absent, not only the major portions of the contemporary climax forest but also some of the more hygrophylic elements now characteristic of the Euxino-Hyrcanian zone (*Juglans*, *Pterocarya*, *Fagus*, *Ulmus scabra*, *Carpinus*) indicating a climate certainly more humid and warmer than the present climate; but the existence of a dry summer period was locally also probable, as was confirmed by the presence of *Olea*, *Quercus suber*, and *Q. ilex*.

### IV.1.4—*Pleistocene*

Without entering anew into detail, the appearance of glacial periods, with which the pluvial phases of Africa were more or less directly (Maley, 1976) associated, have created considerable confusion concerning the relationships of the floras of Mediterranean Africa and the Sahara.

In Mediterranean Africa the existence of drier phases and of more variable climates eliminated a certain number of elements, particularly the major segment of present Hyrcano-Euxinian or Macaronesian types. The cold phases and the establishment of glaciers on the high mountains permitted the establishment (despite the persistence of the Strait of Gibraltar) of a certain number of circumboreal elements. Finally, the extension of the steppes, especially *Artemisia* and Chenopodiaceae, appeared to be a phenomenon generally associated with the increase of continental climates begun at the end of the cataglacial phases. If several glacial periods of variable nature followed upon each other in North Africa, it appears very probable that the last one was the most intense, as the study of the flora and especially of the residual or relic floras clearly shows.

In the Sahara, the impact of pluvial phases on the flora and the vegetation in the Pleistocene has been considerable (Rognon, 1976). Just as we have shown for the last one on fossil guano of *Procavia*, which it is impossible to impute to wind dispersal (Pons & Quézel, 1956, 1957; Quézel & Martinez, 1958, 1961), the increase in precipitation wiped out a great part of the desert and permitted the exchange of species between the Mediterranean and tropical regions. This phenomenon, cyclic during the Pleistocene, affected profound changes in the pattern of the floristic domains and in the migrations of the flora, the interpretation of which has not always been clear; I shall return to this question later.

## IV.2—PROBLEMS RELATIVE TO THE ESTABLISHMENT OF THE PRESENT FLORAS (Fig. 11)

For greater ease I shall examine these problems successively in terms of the biogeographical origin of the different elements.

### IV.2.1—*Mesogean Elements*

I am uniting under this term at the same time Mediterranean, Irano-Turanian, and Saharo-Arabian taxa. All these conform to climatic criteria, among which the presence of an essentially summer dryness (sometimes replaced by a nearly constant dryness for the Saharan taxa) is the major characteristic; the distinction between the Mediterranean and Irano-Turanian elements is especially of geographical origin since the thermal criteria (Daget, 1977; Nahal, 1976) are not determinants.

If the existence of a period of annual dryness is probable (we have seen that

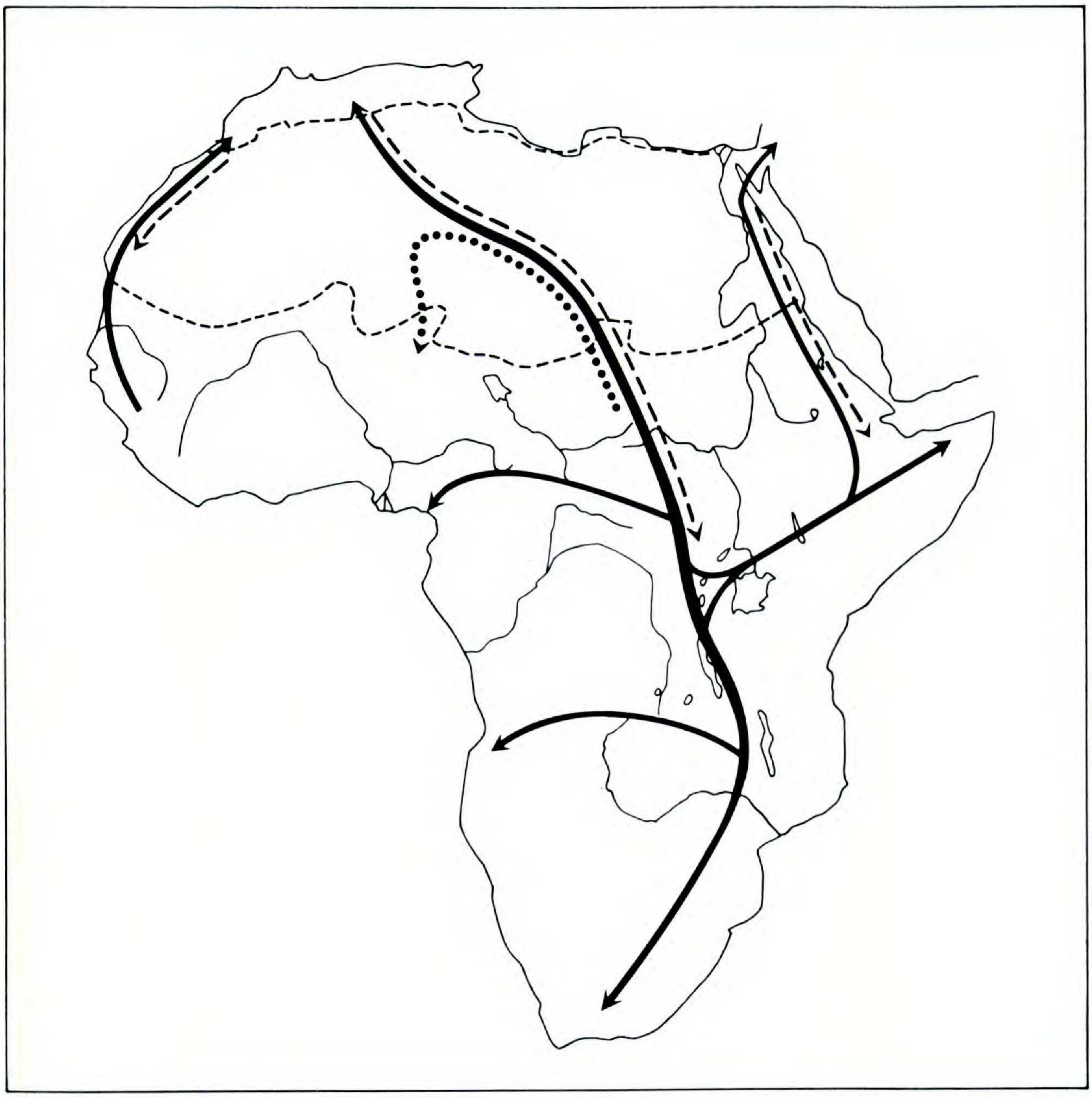

FIGURE 11. Migration routes in Africa (Pliocene and Pleistocene). Heavy dark arrow: tropical elements; dotted arrow: Southern Saharan orophilic elements; dashed arrow: Mediterranean elements.

it has existed since the Pleistocene), it is not obvious that a precipitation regime of the Mediterranean type (Axelrod, 1973) existed at this period. It would most certainly have appeared in the Pleistocene, connected with the initiation of the glacial phases. According to Axelrod, this climate would have been only periodic during this period.

The contributions relating to the perturbations caused by the glaciations on the Mediterranean flora are beginning to be well known, and have revealed themselves to be very remarkable.

Under these conditions, the Mesogean floristic assemblage has since its inception, undergone incessant onslaughts, especially climatic, which render global interpretation difficult but which have in every way greatly favored speciation.

IV.2.1.1—*Sources of the Mesogean Flora.*—Sources of the Mesogean flora are many, both Eurasian (indeed Laurasian) and African.

The Eurasian elements, whose arrival in Africa did not appear to be prior to the disappearance of the Tethys at the Neogene, are composed of numerous types common to Europe and North America (Raven, 1973), but also often to north-tropical Asia (Meusel, 1971), doubtlessly dating from the Cretaceous; at least their common ancestors had evolved before the separation of these two continents. Here are found at one and the same time elements of the temperate forests designated above, a great deal of which is still present in North Africa, but also elements which are clearly more xeric (particularly *Salvia*, *Lavatera*, *Berberis*, *Smilax*, *Arbutus*, *Rhamnus*, and various Cistaceae). These two floristic types had certainly been present in North Africa during the second part of the Tertiary, and the first was in part eliminated at the time of the climatic modification connected with the beginning of the glaciations. The Euxyno-Hyrcanian and Macaronesian elements had by then been extremely reduced and only traces of it have persisted. On the Constantino-Tunisian coast, always very humid, can be noted *Chrysosplenium dubium*, *Epimedium perralderianum*, *Quercus afares*, and on the Moroccan oceanic coast (at least for the true Macaronesian taxa of indisputable Mesogean origin) *Asparagus*, *Chenolea*, *Helianthemum*, *Hypericum*, *Rhus*, *Lithospermum*, *Andryala*, (and indeed Laurasian), *Drusa*, and *Cneorum*.

This flora, Eurasian in origin and certainly evolved on the northern side of the Tethys, has become widespread over the whole of the true Mediterranean region, but also more to the east even to oriental Asia. The xeric types whose appearance doubtlessly goes back to the more or less cyclic dry periods, which date from the middle of the Miocene (Andreànszky, 1963; Demangeon, 1958) and which have been substantiated by a certain number of macro or fossil pollen (Pons, 1964), have profited in addition from the elevation of the Mesogean mountain massifs. It is certainly from this period that the establishment of orophilic taxa extending from the Atlantic to the Himalayas must be dated; the greater part of these have given birth to endemic vicariate series. Examples of this are genera like *Cedrus*, *Abies*, and *Berberis*, the arborescent *Juniperus* of the Mediterranean, as well as the major part of the elements actually considered as oro-Mediterranean (Quézel, 1957).

These elements have contributed a great deal to the evolution of the Mediterranean flora, especially the sclerophyllous forest, since the Pliocene where, according to Axelrod & Raven (1978), it occupied a large part of the Maghreb and the northern Sahara and reached the mountain massifs of the central Sahara. The elements of tropical origin (cf. below) were largely associated with it. It appears, however, that from the middle Pliocene there may have developed a state of aridity on the southern margins that leads me to agree with the results cited below for Koro-Toro (Coppens & Koeniguer, 1976).

During the Pleistocene, and certainly during several reprieves, the alternation of the truly arid desert phases with wetter phases in the whole of the true Sahara has affected interesting migrations of the floras. The example of the last pluvial phase can give us a good idea of this (Quézel & Martinez, 1961). Under these conditions Mediterranean taxa could have survived in certain localities, particularly on the Saharan mountains, side by side with other elements of African origin. The existence of several such fluctuations is the reason why a certain level of endemism is evident in this flora. The most remarkable example is that of *Cupressus dupreziana*, at least for the strains of Mesogean origin. On the contrary, as we have indicated (Bruneau de Miré & Quézel, 1961) *Olea laperrini* and *Myrtus nivellei* belong to the montane African strains.

IV.2.1.2—*The True Saharo-Arabian Flora.*—The flora truly considered to be Saharo-Arabian and therefore of northern origin, could only have evolved following the establishment of dry phases forming true deserts. It does not seem possible, as I discussed earlier, to place the start of this phenomen in North Africa before the Pliocene, but its extension into the Sahara was certainly concomitant with the glacial phases, especially the appearance of interpluvial phases, of which the present one appears to be the most intense (Quézel, 1958). The Saharo-Arabian taxa belonging to the Mesogean flora are numerous. This is the situation particularly for those that belong to the Crucifereae, Caryophyllaceae, Resedaceae, Boraginaceae, Leguminosae (p.p.), Tamaricaceae, and Umbelliferae but also to the Zygophyllaceae, and to a part of the Leguminosae, as well as the Gramineae. The existence of a certain number of taxa common to the African desert and the American desert: *Fagonia, Zygophyllum, Frankenia, Oligomeris* (Raven, 1973), likewise points in favor of a more precocious differentiation of certain taxa. It is always difficult to set a limit between the Saharo-Arabian elements and those which belong for the most part to the "Rand Flora," and whose origin is African (cf. below). Endemism is quite important in this flora and the relative antiquity of its establishment in the Sahara is confirmed.

IV.2.1.3—*The Irano-Turanian Flora.*—This flora enjoys only a minor role in North Africa. It characterizes the steppes and continental deserts with hot summers and very cold winters, climatic characteristics very close to those proposed by Adam (1969) to characterize the end of the glacial phases of the Quaternary. It is in fact very probable that this type of climate has been able to persist elsewhere on mountain massifs, even during the course of the interglacial periods, and which has conditioned the appearance of this flora from preexisting taxa, especially the Salsolaceae, Leguminosae (*Astragalus*), and Compositae (*Artemisia*). The Ephedraceae have also benefitted much from this type of climate.

If it is presently in eastern and central Asia that the Irano-Turanian flora reaches its optimal development, it is appropriate to remember that in the present Mediterranean region the retreat of the glaciers has, in a way, brought about an almost constant expansion of a pollen flora of this type during several thousand years, based particularly on Salsolaceae, Ephedraceae and *Artemisia* (Reille, 1975; de Beaulieu, 1977), which also appeared on the Atlas Mountains (Reille, 1976) and which is difficult not to associate with a climatic type of the present Irano-Turanian type. Some quite similar climatic conditions persist in North Africa on the high mountains and plateaus, which have likewise permitted, even to our day, the maintenance of a certain number of its representatives. Endemism has been much reduced here, and this testifies to the recent development of this flora, whose different elements could nevertheless have persisted since the initiation of the glacial phases on the high mountains (Atlas Mountains), where several endemics (*Artemisia*, spiny *Astragalus*) have evolved.

IV.2.1.4—*African Elements in the Mesogean Flora.*—The Mediterranean flora of North Africa appears at first glance to have only remote connections with the flora of African origin which, however, had occupied these territories in the Paleogene, and even during a part of the Neogene. In fact, a closer examination shows that this interpretation deserves to be modified slightly.

In effect, if one makes an exception of the recent immigrants cited above—these doubtlessly participating accidentally, especially in the case of hygrophilous or anthropophilous species—it is possible to associate a certain number of groups of species now present in North Africa with the African flora.

The first is that of species present at the same time in the savannas of Africa, certain mountains of the Sahara, and the Mediterranean region (at least in part). This is the case particularly for the Gramineae, especially the Andropogoneae noted earlier, which as a group have not changed from a taxonomic view over their entire area of distribution. For this reason I do not think that their occurrence in the Mediterranean region or in the Sahara is ancient; this certainly happened during the Quaternary pluvial phases, which permitted an intermeshing of Mediterranean and tropical assemblages in different spots. These exchanges have been brought about on several occasions during the course of the Pleistocene, but the thermal demands, relatively large for these species, permitted them to become established and to persist in the Mediterranean region, where they are, however, confined to the warmest zones (Thermo-Mediterranean Stage; Ozenda, 1975; Quézel, 1976). On the contrary, the Sahelian species characteristic of the "Desert Savanna," e.g., *Acacia panicum* (Maire, 1940; Quézel, 1965) from all evidence penetrated into the Sahara only at the end of the last pluvial stage (doubtlessly after several other phases of extension) but did not reach the Mediterranean regions because of their thermal demands.

A second interpretation is precisely that of the "Rand Flora." This ancient eremic African flora, perhaps earlier than the Oligocene, is difficult to assess, especially because of the exchanges which could have occurred across Africa, notably in the Pliocene, with the Saharo-Arabian flora. We have already supplied a possible list above, but it is necessary to recall that a part of the true Macaronesian flora could have been related to it, especially the crassulescent or succulent elements (Fig. 7).

In fact, a large number of Saharan genera have a north-south tropical distribution in Africa, and it is possible that new research will again expand this list. Here may be noted again the genus *Pituranthos* which has 2 species in Namaqualand, as well as *Zygophyllum*, *Mesembryanthemum*, *Tribulus*, *Cleome*, and *Suaeda*.

The presence in the American desert of elements usually connected to this flora should be noted and certainly verifies the antiquity of its establishment.

Examples are *Oligomeris*, *Talinum*, *Trianthema*, and also perhaps *Fagonia*, *Boerhavia*, and *Cleome*.

A third group is made up of species whose present distribution is indisputably Mediterranean, but which belong to essentially tropical genera. Raven (1973) believes and emphasizes, rightly so, that these taxa are not extant in America, and that their evolution and the migration into the Mediterranean region must therefore have taken place after the separation of these continents. It would not have been prior to the Miocene. It also is highly probable that a certain number of representatives of the vegetation of African origin which had developed before the effacement of the Tethys, particularly in North Africa, could have lived there or formed types adapted to the new climatic conditions. Such seems particularly to be the case for the genera *Olea*, *Ceratonia*, *Tetraclinis*, *Chamaerops*, *Laurus*, *Myrtus*, *Ficus*, *Maytenus*, and *Capparis*.

In fact, there was also the possibility of exchange between the Cape and Mediterranean regions. Burtt (1971) supplies several examples of this, and even if certain ones can be interpreted as anthropozoogenic, it is clear that the present distribution of the genera *Erica* (Fig. 8), *Lotononis*, *Helichrysum*, and *Pentzia*, as well as the section *Hastati* of the genus *Rumex* (Meusel, 1971) cannot be interpreted differently. The existence of genera from all evidence vicariants again confirms this, together with the antiquity of the separation. This is the case for the genera *Echium*, *Thymelaea*, *Iris*, *Mercurialis*, and *Buxus*, represented in South Africa by the genera *Echiostachys*, *Passerina*, *Moraea*, *Seidelia*, and *Notobuxus*. Among the Fumariaceae the affinities between the genera *Rupicapnos* and *Trigonocapnos*, *Platycapnos* and *Discocapnos*, *Sarcocapnos* and *Cysticapnos* should be noted.

IV.2.2—*Northern Elements*

I include in this term the floristic elements of European, Eurasian paleotemperate, or circumboreal origin.

In fact, it appears that originally the majority of these were not separate from certain constituents of the true Mesogean flora, and I have discussed this previously. It is evident that the climatic fluctuations experienced since the Pliocene have greatly modified the representation of species belonging to this biogeographical type. The dry Pliocene phases in part weakened it, and the same thing happened during the glacial periods, at least for the types most sensitive to cold and dryness. On the other hand, the glaciations in North Africa permitted the appearance of a number of circumboreal or new alpine elements, especially on the Atlas Mountains, via the Iberian Peninsula (Quézel, 1957). A migration by the Sicilian-Tunisian bridge was equally possible and would explain the presence in the northeastern Maghreb of a certain number of taxa of European origin.

Several lineages which are doubtlessly related to these elements have even reached the mountains of the Tibesti, but here it is a question of hygrophilic or indeed clearly heliophilic species or truly xerophilic species (cf. above). In my opinion their appearance on this massif could not have been prior to the Pleistocene, at least based on our present state of knowledge.

IV.2.3—*Tropical Elements*

Autochthonous in North Africa and in the Sahara after the Paleocene, indeed after the Cretaceous, they have been progressively eliminated from them by the climatic transformations which came about after the end of the Miocene, as well as by the glacial episodes of the Pleistocene which assured the quasi-defintive destruction of them. In fact, as mentioned above, the tropical elements still play an obvious role in the flora known as "Mesogean" and I will not return to this matter.

It is still necessary to consider here the question of the survival, essentially on the Saharan mountains, but also on the maritime fringes of the Sahara—indeed of Mediterranean Morocco—of an important group of tropical elements, for the most part with montane affinities, which pose the problem of the persistence "in situ" of certain elements belonging to this biogeographical type.

*The Moroccan Coast.*—It has already been discussed with respect to the Macaronesian element and a part of this element is very near, if not the same, as the "Rand Flora." However, this position should not be generalized; some Moroccan endemics of tropical origin are probably better considered to be differentiated vestiges, "in situ" doubtlessly since the Pleistocene. The most remarkable case is certainly that of *Acacia gummifera*, sole representative of the genus adapted to the Mediterranean climate. *Andrachne* and *Commelina rupicola* could also be cited.

*The Red Sea Coast.*—I have already discussed this and it will suffice to stress the presence here of an appreciable number of taxa of African montane affinity, but which do not appear to be cases of endemism. This phenomenon is without doubt connected with the fact that these populations are always in contact, through the Sudanese coastal mountain chains, particularly the Erkowit Mountains, with the flora of the Ethiopian plateaus. One can also envision a recent establishment, which is in fact in contradiction with the paleoclimatic data.

*The Mountains of the Central Middle Sahara.*—The thorough exploration of Hoggar (Maire, 1940; Quézel, 1954), of Tibesti (Maire & Monod, 1950; Quézel, 1954), of Air (Bruneau de Miré & Gillet, 1956), of Ennedi (Carvalho & Gillet, 1960), of Jebel Gourgeil (Quézel, 1969), of Jebel Marra (Wickens, 1977), has brought to light a whole flora of African origin which appears to represent well the traces of the flora which colonized these massifs before the appearance of the severe desert formations which characterize the southern Sahara today.

If this flora is still incompletely known, and certain taxonomic revisions appear desirable, it is nevertheless possible to discern there at least their groups: a montane African group, an autochthonous montane group, and a group of oro-African origin.

I shall not review here the list of species which are associated with them, the affinities which may relate certain taxa to the "Rand Flora." I shall note, however, that *Tibestina lanuginosa*, described by Maire as endemic to Tibesti, corresponds in fact (Scholz, 1966) to *Dicoma capensis* of southern Africa and *Eleocharis tibestica* (Quézel, 1959) to *E. intricata* of Madagascar and southern Africa.

On the other hand, from the point of view of categorizing taxa, it appears possible to associate the first two of these groups, more or less directly to the "montane rain forest" (sensu Greenway, 1970), whose appearance on the mountains of the Sahara, can be traced back to the Paleocene; according to Greenway, however, its extension on the other African massifs dates more from the Miocene.

Although that is possible, one cannot pin down the position of this flora to this period; migrations have actually been possible during the pluvial phases of the Pleistocene, a period which really appears to correspond with the differentiation and development of the oro-African flora.

In fact, one can question whether the montane axes of Africa (cf. Fig. 11) have not constituted a route of temporary migration for the various African floras. The results published by Sah (1967) for pollen derived from the region of Lake Kivu and doubtlessly dating from the end of the Pliocene seems to confirm this, since many tropical families still present in part on the Jebel Marra, and indeed Tibesti, appear there, as well as families with more temperate affinities (Cruciferae, Buxaceae, Ericaceae, Geraniaceae). It is certainly via this route that the majority of exchanges between the African highland flora—and indeed the Cape flora—and the flora of the present Mediterranean region have been brought about. The "Rand Flora," as well as the present Macaronesian flora to which it is related, without a doubt benefitted equally from this migration route, which finally was only closed periodically during the Pleistocene especially during the interpluvial phases.

## V. Conclusions

This analysis of the Mediterranean and Saharan flora permits me to draw a certain number of conclusions, particularly if one attempts at the same time to interpret the origin of the phytogeographic elements that exist there.

I have stressed above the principal differences which can be observed between the Mediterranean and the Saharan floras in terms of representation and number of genera, percentage of endemics, or as a function of the present distribution of geographical types; I will not return to this.

It is, on the other hand, interesting to emphasize that the general effect of the flora points to a relatively recent origin since the original stocks did not differentiate, primarily "in situ" but well to the south of the northern side of the Tethys. The appearance of the Mesogean flora in Africa seems, on the whole, to have been contemporary with the upper Miocene.

From the viewpoint of climate, the replacement of a climate of a truly equatorial or tropical type by a more variable regime having dry periods seems to date essentially from the Pliocene, at least in the true Saharan region; more to the north, relatively dry periods appear to have already existed in the Miocene.

In fact, it is becoming clearer that the Mesogean flora ought to be considered as a flora of discrete additions provided at the same time from Eurasian and tropical elements, which evolved in and migrated from very distinct climatical and geomorphological environments, and which have been disclosed as being eminently favorable in every way to the phenomenon of speciation. It is probable that the climatic instability already evident in the Miocene and especially in the Pliocene, and exacerbated during the Pleistocene, has been a determining factor in the appearance of numerous species. This phenomenon has again been favored by orogenic phases which followed upon each other during the second part of the Tertiary in this entire region.

On the contrary, the differentiation of the Mediterranean, Saharan, and Irano-Turanian bioclimatic entities seems to be directly associated with great climatic fluctuations in the Pleistocene which finally, and doubtlessly with several lulls, redistributed in the area a relatively homogenous floristic base, at least as to its origin.

The tropical element, a part of which has participated in the formation of the floristic base of the Mesogean since its inception, has always been largely eliminated from Mediterranean Africa for essentially climatic reasons; these have always partly continued to exist in the Macaronesian zone, even though they have been decimated by the desertification of the mountains in the present southern Sahara. Certain elements, especially adapted elements such as the Sahelian flora and the eremic African flora, have continued to enjoy an appreciable role in portions of the Sahara that continue to benefit periodically from rains of the tropical front.

All these conditions have been favorable, theoretically at least, to the development of a rich and diversified flora; the number of endemics of the African Mediterranean zone (a little less than 30%) really shows this. In the Sahara the climatic rigor and also an excessive climatic instability during the Pleistocene have limited this phenomenon (about 12%). It is also certain that it is the therophytes which have most broadly benefitted from this climatic context, since they represent about 50% of the Mediterranean flora in North Africa and also of the Saharan flora. These high percentages have only been surpassed by those which appear in the area of the northern Sahelian flora where they reach almost 70% (Quézel, unpublished). It is, moreover, among the therophytes that endemism is equally high. This phenomenon is above all evident in the typically Mediterranean families: Caryophyllaceae (nearly 60% of the annual species are endemic), Cruciferae (more than 70% of the species and 11 genera are endemic), Resedaceae, Umbelliferae, and Scrophulariaceae.

It is also interesting to note in the matter of endemics that in the Mediterranean region, North Africa has especially benefitted from the functioning of the Ibero-Mauritanian zone, or better, Ibero-Moroccan, through which more than 500 of the endemic species presently recorded in North Africa were formed. This figure is doubled if one adds to these the Ibero-Mauritanian species. On the other hand, west-central Algeria and Tunisia have only a very intermediate percentage of endemism, at least at the circum-Mediterranean level; the case of Cyrenia is not very different, although this region has profitted more from endemics of Mideastern origin.

In the Sahara, apart from the endemics of the northwestern Sahara which reveal at least in part an Ibero-Moroccan influence, and some highly residual species, the endemic species are generally much more widely distributed, doubtlessly because of the climatic and geomorphological homogeneity (at least in the northern part of the Sahara for the latter). Besides endemism, and perhaps more remarkable, is the existence here of residual and biogeographically very diversified floras. This phenomenon, although largely masked today by extreme aridity little compatible with the development of plant life, reflects in fact the constant climatic disturbances that have assailed this region since the end of the Tertiary and which, with several lulls, have been able to modify the plant life totally.

In place of the idea of a "Saharan barrier," a myth which has persisted tenaciously in the thinking of a great number of phytogeographers up to recent times, it is appropriate to substitute the idea of a space periodically and transitorially desert. This Sahara, in the Neogene and at different times in the Pleistocene, has, locally at least, functioned as a favored place of exchanges between the African and Mesogean floras. But it still remains at the present time, and in spite of a climate particularly unfavorable throughout its entirety, a veritable conservatory for certain taxa which have followed each other since the end of the Miocene.

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